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Fungal strategies for dealing with environmental and agricultural stress

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Abstract

The Fungal Kingdom is responsible for many ecosystem services as well as many industrial and agricultural products. Nevertheless, how these fungal species function and carry out these services is dependent on their capacity to grow under different stress conditions caused by a variety of abiotic factors such as ionizing radiation, UV radiation, extremes of temperature, acidity and alkalinity, and environments of low nutritional status, low water activity, or polluted with, e.g. toxic metals or xenobiotics. This article reviews some natural or synthetic environments where fungi thrive under stress and have important impacts in agriculture and forestry.

Key words: ionizing radiation, biotic stress, UV radiation, growth promotion, mediation of plant stress, aeromicrobiology

Introduction

Fungi are responsible for many industrial and agricultural products or processes as well as many ecosystem services **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. However, many of the environments where fungi provide these services or products are under extreme stress. For example, to produce ethanol, the yeast *Sacharomyces cerevisiae* needs to cope with high ethanol concentrations, oxidative and osmotic stress as well as high temperatures generated by fermentation **{** ADDIN EN.CITE <EndNote><Cite><Author>Eleutherio</Author><Year>2015</Year><RecNum>8535</RecNum><record><rec-number>8535</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8535</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Eleutherio, Elis</author><author>Panek, Anita</author><author>De Mesquita, Joelma Freire</author><author>Trevisol, Eduardo</author><author>Magalhães, Rayne</author></authors></contributors><titles><title>Revisiting yeast trehalose metabolism</title><secondary-title>Current Genetics</secondary-title></titles><periodical><full-title>Current Genetics</full-title></periodical><pages>263-274</pages><volume>61</volume><number>3</number><dates><year>2015</year><pub-dates><date>2015//</date></pub-dates></dates><isbn>1432-0983</isbn><urls><related-urls><url>http://dx.doi.org/10.1007/s00294-014-0450-1</url></related-urls></urls><electronic-resource-num>10.1007/s00294-014-0450-1</electronic-resource-num></record></Cite></EndNote>**}**. Therefore, fungi must be able to respond adequately to the stress conditions to provide microbial services and products.

“Fungal stress” is a rather diffuse term { ADDIN EN.CITE <EndNote><Cite><Author>Ortiz-Urquiza</Author><Year>2015</Year><RecNum>8355</RecNum><record><rec-number>8355</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8355</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Ortiz-Urquiza, Almudena</author><author>Keyhani, Nemat O.</author></authors></contributors><titles><title>Stress response signaling and virulence: insights from entomopathogenic fungi</title><secondary-title>Current Genetics</secondary-title></titles><periodical><full-title>Current Genetics</full-title></periodical><pages>239-249</pages><volume>61</volume><number>3</number><dates><year>2015</year></dates><isbn>1432-0983</isbn><label>Ortiz-Urquiza2015</label><work-type>journal article</work-type><urls><related-urls><url>http://dx.doi.org/10.1007/s00294-014-0439-9</url></related-urls></urls><electronic-resource-num>10.1007/s00294-014-0439-9</electronic-resource-num></record></Cite></EndNote>}. When is a fungal cell exposed to stress? Is every deviation from optimal growth in fact “stress”, and does the terminology “suboptimal” imply that a cell is under stress? Alternatively, maximal (“optimal”) growth impinges on all metabolic pathways of the cell and stretches the physiology of the cell to its limits. One can imagine that even this state of a cell can be interpreted as stress.

The term “stress” in mycology refers to those situations that restrict or prevent the growth and reproduction of fungi. The classical language of biology has two expressions- namely *stimulus* to describe change in environment and *response* to describe the resulting change in the organism **{** ADDIN EN.CITE <EndNote><Cite><Author>Jennings</Author><Year>1993</Year><RecNum>8436</RecNum><record><rec-number>8436</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8436</key></foreign-keys><ref-type name="Edited Book">28</ref-type><contributors><authors><author>Jennings, D. H.</author></authors><secondary-authors><author>Lemke, P. A.</author></secondary-authors></contributors><titles><title>Stress Tolerance of Fungi</title><secondary-title>Mycology Series</secondary-title></titles><pages>281</pages><volume>10</volume><number>II</number><dates><year>1993</year><pub-dates><date>1993</date></pub-dates></dates><pub-location>New York</pub-location><publisher>Marcel Dekker, Inc.</publisher><urls></urls></record></Cite></EndNote>**}**. Classical heat shock response studies revealed two fundamental features: first, mild stress - which is the *stimulus* and second, the *response* which is the induction of a higher level of resistance **{** ADDIN EN.CITE <EndNote><Cite><Author>Hohmann</Author><Year>2003</Year><RecNum>7224</RecNum><record><rec-number>7224</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">7224</key></foreign-keys><ref-type name="Book">6</ref-type><contributors><authors><author>Hohmann, S.</author><author>Mager, W.H.,</author></authors></contributors><titles><title>Yeast Stress Responses</title></titles><dates><year>2003</year></dates><pub-location>Berlin</pub-location><publisher>Springer-Verlag</publisher><urls></urls></record></Cite><Cite><Author>Rangel</Author><Year>2011</Year><RecNum>6739</RecNum><record><rec-number>6739</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">6739</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Rangel, D.E.N.</author></authors></contributors><titles><title>Stress induced cross-protection against environmental challenges on prokaryotic and eukaryotic microbes</title><secondary-title>World Journal of Microbiology & Biotechnology</secondary-title><alt-title>World J. Microbiol. Biotechnol.</alt-title></titles><periodical><full-title>World Journal of Microbiology & Biotechnology</full-title><abbr-1>World J Microb Biot</abbr-1></periodical><alt-periodical><full-title>World J. Microbiol. Biotechnol.</full-title></alt-periodical><pages>1281-1296</pages><volume>27</volume><dates><year>2011</year></dates><urls><related-urls><url>http://link.springer.com/article/10.1007%2Fs11274-010-0584-3</url></related-urls></urls><electronic-resource-num>10.1007/s11274-010-0584-3</electronic-resource-num></record></Cite></EndNote>**}**. This feature seems to be universal, and has even resulted as an "evolutionary Pavlovian conditioning response" for stresses that can be predicted **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. Environmental, cellular, and molecular aspects of stress effects and responses in yeasts and filamentous fungi have been reviewed by Avery et al. **{** ADDIN EN.CITE <EndNote><Cite ExcludeAuth="1"><Author>Avery</Author><Year>2008</Year><RecNum>8101</RecNum><record><rec-number>8101</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8101</key></foreign-keys><ref-type name="Book">6</ref-type><contributors><authors><author>Avery, S.V.</author><author>Stratford, M,</author><author>van West, P.</author></authors></contributors><titles><title>Stress in Yeasts and Filamentous Fungi</title></titles><pages>306</pages><dates><year>2008</year></dates><pub-location>Amsterdam</pub-location><publisher>Elsevier</publisher><urls></urls></record></Cite></EndNote>**}**. There is increasing awareness that stress may arise not only in natural systems subject or not to anthropogenic impact, but also under the comparatively controlled conditions of fungal culture.

Stressful environments in which fungi thrive

Fungi are ubiquitous components of the microbial communities of any terrestrial environment, including such hostile habitats as the Arctic, hot deserts, and metal-rich and hypersaline soils (Burford *et al*. 2003). Fungi are also ubiquitous in habitats polluted by xenobiotics, toxic metals and radionuclides, as well as leachates and other solid or liquid wastes (Fomina *et al*. 2005). Appreciation of fungi as agents of geochemical change is growing, and their significance is being discovered even in locations not usually regarded as prime fungal habitats, e.g. rocks, acid mine drainage, deep aquatic sediments, hydrothermal vents and the igneous oceanic crust (Reitner *et al*. 2006; Gorbushina 2007; Vázquez-Campos *et al*. 2014; Ivarsson *et al*. 2016). In such habitats, fungi may exhibit a variety of mechanisms that determine tolerance and survival. These “extreme” locations may also act as a reservoir of novel organisms with unusual properties (Selbmann *et al*. 2013). Fungal strategies for dealing with environmental stress are interlinked with their ability to adopt a variety of growth, metabolic and morphological strategies, adaptive capabilities to environmental extremes and, their symbiotic associations with animals, plants, algae and cyanobacteria (Burford et al. 2003; Gadd 2004; Selbmann *et al*. 2013).

***Atmosphere*:** Fungi can be metabolically active in extreme habitats. One of the most extreme habitats in which fungi survive is the atmosphere, where low temperatures, low amounts of nutrients, extreme desiccation, and extreme ultraviolet radiation are found. Despite this, viable fungi have been isolated from aeroplanes **{** ADDIN EN.CITE <EndNote><Cite><Author>Holzapfel</Author><Year>1978</Year><RecNum>7644</RecNum><record><rec-number>7644</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">7644</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Holzapfel</author></authors></contributors><titles><title>Transoceanic airplane sampling for organisms and particles</title><secondary-title>Pacific Insects</secondary-title></titles><periodical><full-title>Pacific Insects</full-title></periodical><pages>169-189</pages><volume>18</volume><dates><year>1978</year></dates><urls></urls></record></Cite></EndNote>**}**, stratospheric balloons **{** ADDIN EN.CITE

<EndNote><Cite><Author>Harris</Author><Year>2001</Year><RecNum>7984</RecNum><record><rec-number>7984</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">7984</key></foreign-keys><ref-type name="Book Section">5</ref-type><contributors><authors><author>Harris, M. J.</author><author>Wickramasinghe, N. C.</author><author>Lloyd, D.</author><author>Narlikar, J. V.</author><author>Rajaratnam, P.</author><author>Turner, M. P.</author><author>Al-Mufti, S.</author><author>Wallis, M. K.</author><author>Ramadurai, S.</author><author>Hoyle, F.</author></authors><secondary-authors><author>Hoover, R. B.</author><author>Levin, G. V.</author><author>Paepe, R. R.</author><author>Rozanov, A. Y.</author></secondary-authors></contributors><titles><title>The detection of living cells in stratospheric samples</title><secondary-title>Instruments, Methods, and Missions for Astrobiology Iv</secondary-title><tertiary-title>Proceedings of the Society of Photo-Optical Instrumentation Engineers (Spie)</tertiary-title></titles><pages>192-198</pages><volume>4495</volume><dates><year>2001</year></dates><isbn>0277-786X
0-8194-4209-7</isbn><accession-num>WOS:000175125700019</accession-num><urls><related-urls><url><Go to ISI>://WOS:000175125700019</url></related-urls></urls></record></Cite></EndNote>}, and rockets { ADDIN EN.CITE { ADDIN EN.CITE.DATA }} from 10 to 50 km altitude in the stratosphere and 50 to 100 km above the Earth in the mesosphere { ADDIN EN.CITE { ADDIN EN.CITE.DATA }}. Fungi possessing black conidia (*Aspergillus niger*) and green conidia (*Penicillium notatum*)

were collected from a rocket that reached the mesosphere at an altitude of 48 to 77 km {
ADDIN EN.CITE
<EndNote><Cite><Author>Imshenetsky</Author><Year>1978</Year><RecNum>7680</RecNum><record><rec-number>7680</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">7680</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Imshenetsky, A. A.</author><author>Lysenko, S. V.</author><author>Kazakov, G. A.</author></authors></contributors><titles><title>Upper boundary of the biosphere</title><secondary-title>Appl Environ Microbiol</secondary-title></titles><periodical><full-title>Appl Environ Microbiol</full-title></periodical><pages>1-5</pages><volume>35</volume><number>1</number><edition>1978/01/01</edition><keywords><keyword>*Air Microbiology</keyword><keyword>*Air Movements</keyword><keyword>*Altitude</keyword><keyword>Bacteria/growth & development/radiation effects</keyword><keyword>Fungi/*growth & development/radiation effects</keyword><keyword>Pigmentation</keyword><keyword>Species Specificity</keyword><keyword>Ultraviolet Rays</keyword></keywords><dates><year>1978</year><pub-dates><date>Jan</date></pub-dates></dates><isbn>0099-2240 (Print)
0099-2240 (Linking)</isbn><accession-num>623455</accession-num><urls><related-urls><url>http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubM

ed&dopt=Citation&list_uids=623455</url></related-urls></urls><custom2>242768</custom2><language>eng</language></record></Cite></EndNote>**}**. Since Antonie van Leeuwenhoek **{** ADDIN EN.CITE <EndNote><Cite><Author>van Leewenhoeck</Author><Year>1677</Year><RecNum>7145</RecNum><record><rec-number>7145</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">7145</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>van Leewenhoeck, Antony</author></authors></contributors><titles><title>Observations, communicated to the publisher by Mr. Antony van Leewenhoeck, in a Dutch letter of the 9th of Octob. 1676. Here English'd: concerning little animals by him observed in rain-well-sea. and snow Water; as also in water wherein pepper had lain infused</title><secondary-title>Philosophical Transactions</secondary-title></titles><periodical><full-title>Philosophical Transactions</full-title></periodical><pages>821-831</pages><volume>12</volume><number>133-142</number><dates><year>1677</year><pub-dates><date>January 1, 1677</date></pub-dates></dates><urls><related-urls><url>http://rstl.royalsocietypublishing.org/content/12/133-142/821.short</url><url>http://rstl.royalsocietypublishing.org/content/12/133-142/821.full.pdf</url></related-urls></urls><electronic-resource-num>10.1098/rstl.1677.0003</electronic-resource-num></record></Cite></EndNote>**}** and Louis Pasteur **{** ADDIN EN.CITE <EndNote><Cite><Author>Pasteur</Author><Year>1860</Year><RecNum>8081</Re

cNum><record><rec-number>8081</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8081</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Pasteur, L.</author></authors></contributors><titles><title>Expériences relatives aux générations dites spontanées</title><secondary-title>Compt. Rend. Acad. Sci. (Paris)</secondary-title></titles><periodical><full-title>Compt. Rend. Acad. Sci. (Paris)</full-title></periodical><pages>303-307</pages><volume>50</volume><dates><year>1860</year></dates><urls></urls><electronic-resource-num>http://www.academie-sciences.fr/archivage_site/fondations/lp_pdf/CR1860_p303.pdf</electronic-resource-num></record></Cite></EndNote>**}**, microbes have usually been considered passive inhabitants of the atmosphere, dispersing via airborne dust particles. Present studies, however, reveal that bacteria and fungi are metabolically active even under those conditions **{** ADDIN EN.CITE <EndNote><Cite><Author>Amato</Author><Year>2012</Year><RecNum>7595</RecNum><record><rec-number>7595</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">7595</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Amato, P.</author></authors></contributors><titles><title>Clouds provide atmospheric oases for microbes</title><secondary-title>Microbe</secondary-title></titles><periodical><full-title>Microbe</full-title></periodical><pages>119-123</pages><volume>7</volume><number>3</number><dates><year>2012</year></d

ates><urls></urls></record></Cite><Cite><Author>Amato</Author><Year>2007</Year><RecNum>7689</RecNum><record><rec-number>7689</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">7689</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Amato, P.</author><author>Demeer, F.</author><author>Melaouhi, A.</author><author>Fontanella, S.</author><author>Martin-Biesse, A.-S.</author><author>Sancelme, M.</author><author>Laj, P.</author><author>Delort, A.-M.</author></authors></contributors><titles><title>A fate for organic acids, formaldehyde and methanol in cloud water: their biotransformation by micro-organisms</title><secondary-title>Atmos. Chem. Phys. Discuss.</secondary-title></titles><periodical><full-title>Atmos. Chem. Phys. Discuss.</full-title></periodical><pages>5253-5276</pages><volume>7</volume><dates><year>2007</year></dates><urls></urls></record></Cite></EndNote>**}**, and that they act as a surface for the condensation of water vapor in the atmosphere, thus forming clouds **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. Fungi also serve as ice nuclei in clouds, which are required for snow and rainfall **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. Fungal spores may, therefore, potentially influence the hydrological cycle and climate as nuclei for water droplets and ice crystals in clouds, fog, and precipitation **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**.

Oligotrophic conditions**:** There is increasing evidence that in nature, fungi commonly exist in conditions of nutrient depletion. There is a wide range of nutritional heterogeneity within soil, e.g. from the nutrient-rich rhizosphere to habitats containing low amounts of available organic material (Wainwright 1993). Mineral soil in particular can be a poor source of available carbohydrate (Wainwright *et al*. 1991; Wainwright 1993). Despite this, many fungi can maintain growth in soil and other nutrient-limited habitats (Wainwright *et al*. 1991; Wainwright 1993). It has been suggested that these organisms possess characteristics that enable them to utilize low nutrient supplies efficiently including an increased capacity to take up nutrients by possessing a high surface area resulting from sparse but extensive mycelium, high affinity nutrient uptake sites, and translocation of nutrients from a nutrient-rich base (Wainwright 1993; Ritz 1995; Boswell *et al*. 2002; Jacobs *et al*. 2004). Germ tubes and hyphae may be reduced in diameter and length when compared to similar structures in carbon-rich conditions. Nutrients may also be recycled through cryptic growth, where the tips of the hyphae grow at the expense of pre-formed fungal material (Schnurer & Paustian 1986). It is also possible that carbon dioxide and other gases, and volatiles including hydrocarbons, alcohols, aldehydes, ketones and phenols may be scavenged from the environment and act as a source of fungal nutrition (Tribe & Mabadeje 1972; Fries 1973; Wainwright 1993).

It is predictable therefore, that the responses of fungi towards other stresses, e.g. toxic metals and xenobiotics, will be affected by the nutritional status of the habitat. In a low-nutrient environment, there may be a limitation to expression of both direct and indirect mechanisms of tolerance/resistance, as well as effects on metabolism, growth and branching. Toxic metals can have a significant impact on the overall length of the fungal mycelium and branching patterns, with responses being affected by nutrient availability (Ramsay *et al*. 1999). *Trichoderma viride* and *Rhizopus arrhizus* appeared to exhibit 'foraging' modes of growth on low-substrate media with sparse colonies formed (Ritz 1995), and Cu and Cd were capable of disrupting this explorative growth under laboratory conditions resulting in alterations to the distribution of the fungal biomass (Ramsay *et al*. 1999). If manifest in natural environments, such responses may influence success in locating nutrients as well as survival capability.

***Ionizing radiation*:** An extreme man-made habitat with elevated levels of ionizing radiation was created by the atomic bombardments of Hiroshima and Nagasaki in 1945, nuclear power plants accidents such as Three Mile Island in the United States in 1979 **{**

ADDIN EN.CITE <EndNote><Cite><Author>Hultman</Author><Year>2013</Year><RecNum>8050</RecNum><record><rec-number>8050</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8050</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Hultman, N.</author><author>Koomey, J.</author></authors></contributors><auth-address>[Hultman, Nathan] Univ Maryland, Environm Policy Program, Sch Publ Policy, College Pk, MD 20742 USA. [Hultman, Nathan] Brookings Inst, Washington, DC 20036 USA. [Koomey, Jonathan] Stanford Univ, Steyer Taylor Ctr Energy Policy & Finance, Stanford, CA 94305 USA.
Hultman, N (reprint author), Univ Maryland, Environm Policy Program, Sch Publ Policy, College Pk, MD 20742 USA.</auth-address><titles><title>Three Mile Island: The driver of US nuclear power's decline?</title><secondary-title>Bulletin of the Atomic Scientists</secondary-title><alt-title>Bull. Atom. Scient.</alt-title></titles><periodical><full-title>Bulletin of the Atomic Scientists</full-title><abbr-1>Bull. Atom. Scient.</abbr-1></periodical><alt-periodical><full-title>Bulletin of the Atomic Scientists</full-title><abbr-1>Bull. Atom. Scient.</abbr-1></alt-periodical><pages>63-70</pages><volume>69</volume><number>3</number><keywords><keyword>accident</keyword><keyword>cancellation</keyword><keyword>construction</keyword><keyword>Fukushima</keyword><keyword>industry</keyword><keyword>nuclear</keyword><keyword>power</keyword><keyword>power plant</keyword><keyword>reactor</keyword><keyword>Three Mile Island</keyword><keyword>costs</keyword></keywords><dates><year>2013</year><pub-dates><date>May-Jun</date></pub-dates></dates><isbn>0096-3402</isbn><accession-num>WOS:000318250300009</accession-num><work-type>Article</work-type><urls><related-urls><url><Go to ISI>://WOS:000318250300009</url></related-urls></urls><electronic-resource-num>10.1177/0096340213485949</electronic-resource-num><language>English</language></record></Cite></EndNote>**}**, Chernobyl in Ukraine in 1986 **{** ADDIN EN.CITE <EndNote><Cite><Author>Zhdanova</Author><Year>2000</Year><RecNum>647</RecNum><record><rec-number>647</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">647</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Zhdanova, N.N.</author><author>Zakharchenko, V.A.</author><author>Vember, V.V.</author><author>Nakonechnaya, L.T.</author></authors></contributors><titles><title>Fungi from Chernobyl: mycobiota of the inner regions of the containment structures of the damaged nuclear reactor</title><secondary-title>Mycol. Res.</secondary-title></titles><periodical><full-title>Mycol. Res.</full-title></periodical><pages>1421-1426</pages><volume>104</volume><dates><year>2000</year></dates><urls></urls></record></Cite></EndNote>**}**, and Fukushima Daiichi in Japan in 2011 **{** ADDIN EN.CITE <EndNote><Cite><Author>Koarashi</Author><Year>2014</Year><RecNum>8051</RecNum><record><rec-number>8051</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8051</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Koarashi, J.</author><author>Atarashi-Andoh, M.</author><author>Takeuchi, E.</author><author>Nishimura, S.</author></authors></contributors><titles><title>Topographic heterogeneity effect on the accumulation of Fukushima-derived radiocesium on forest floor driven by biologically mediated processes</title><secondary-title>Scientific Reports</secondary-title></titles><periodical><full-title>Scientific Reports</full-title></periodical><volume>4</volume><dates><year>2014</year><pub-dates><date>Oct</date></pub-dates></dates><isbn>2045-2322</isbn><accession-num>WOS:000343989600004</accession-num><urls><related-urls><url><Go to ISI>://WOS:000343989600004</url></related-urls></urls><electronic-resource-num>10.1038/srep06853</electronic-resource-num></record></Cite></EndNote>**}**, as well as other nuclear accidents such as the Goiania accident in Brazil in 1987 { ADDIN EN.CITE <EndNote><Cite><Author>Godoy</Author><Year>1991</Year><RecNum>9003</RecNum><record><rec-number>9003</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">9003</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Godoy, J. M.</author><author>Guimaraes, J. R.</author><author>Pereira, J. C.</author><author>do Rio, M. A.</author></authors></contributors><auth-address>Instituto de Radioprotecao e Dosimetria/CNEN, Rio de Janeiro, Brazil.</auth-address><titles><title>Cesium-137 in the Goiania waterways during and after the radiological accident</title><secondary-title>Health Phys</secondary-title></titles><periodical><full-title>Health Phys</full-title></periodical><pages>99-103</pages><volume>60</volume><number>1</number><edition>1991/01/01</edition><keywords><keyword>*Accidents</keyword><keyword>Animals</keyword><keyword>Brazil</keyword><keyword>*Cesium Radioisotopes</keyword><keyword>Fishes</keyword><keyword>Food Contamination, Radioactive/analysis</keyword><keyword>Radioisotope Teletherapy/instrumentation</keyword><keyword>Water Pollutants, Radioactive/*analysis</keyword></keywords><dates><year>1991</year><pub-dates><date>Jan</date></pub-dates></dates><isbn>0017-9078 (Print)
0017-9078 (Linking)</isbn><accession-num>1983992</accession-num><urls><related-urls><url>http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=1983992</url></related-

urls></urls><language>eng</language></record></Cite></EndNote>**}**. Several studies of fungal resistance to ionizing radiation have been performed **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. *Cryomyces antarcticus*, which occurs endolithically in the McMurdo Dry Valleys of Antarctica, in the fully hydrated state can survive doses of up to 5000 Gray (Gy), and much higher doses in the dried state **{** ADDIN EN.CITE <EndNote><Cite><Author>Selbmann</Author><Year>2017</Year><RecNum>9096</RecNum><record><rec-number>9096</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">9096</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Selbmann, Laura</author><author>Pacelli, Claudia</author><author>Zucconi, Laura</author><author>Dadachova, Ekaterina</author><author>Moeller, Ralf</author><author>de Vera, Jean-Pierre</author><author>Onofri, Silvano</author></authors></contributors><titles><title>Resistance of an Antarctic cryptoendolithic black fungus to radiation gives new insights of astrobiological relevance</title><secondary-title>Fungal Biology</secondary-title></titles><periodical><full-title>Fungal Biology</full-title><abbr-1>Fungal Biol-Uk</abbr-1></periodical><keywords><keyword>Astrobiology</keyword><keyword>Desiccation</keyword><keyword>Melanin</keyword><keyword>Planetary protection</keyword><keyword>Radioprotection</keyword></keywords><dates><year>2017</year><pub-dates><date>2017/11/04/</date></pub-dates></dates><isbn>1878-6146</isbn><urls><related-urls><url>http://www.sciencedirect.com/science/article/pii/S1878614617301496</url></

related-urls></urls><electronic-resource-num>https://doi.org/10.1016/j.funbio.2017.10.012</electronic-resource-num></record></Cite></EndNote>**}** and are among the most radioresistant organisms on the planet, along with the bacterium *Deinococcus radiodurans* **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**,and an animal tardigrade **{** ADDIN EN.CITE <EndNote><Cite><Author>Horikawa</Author><Year>2006</Year><RecNum>8096</RecNum><record><rec-number>8096</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8096</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Horikawa, Daiki D.</author><author>Sakashita, Tetsuya</author><author>Katagiri, Chihiro</author><author>Watanabe, Masahiko</author><author>Kikawada, Takahiro</author><author>Nakahara, Yuichi</author><author>Hamada, Nobuyuki</author><author>Wada, Seiichi</author><author>Funayama, Tomoo</author><author>Higashi, Seigo</author><author>Kobayashi, Yasuhiko</author><author>Okuda, Takashi</author><author>Kuwabara, Mikinori</author></authors></contributors><titles><title><style face="normal" font="default" size="100%">Radiation tolerance in the tardigrade </style><style face="italic" font="default" size="100%">Milnesium tardigradum</style></title><secondary-title>International Journal of Radiation Biology</secondary-title></titles><periodical><full-title>International Journal of Radiation Biology</full-title></periodical><pages>843-848</pages><volume>82</volume><number>12</number><dates><year>2006</year></dates><urls><related-

urls><url>http://informahealthcare.com/doi/abs/10.1080/09553000600972956</url></related-urls></urls><electronic-resource-num>doi:10.1080/09553000600972956</electronic-resource-num></record></Cite></EndNote>**}**. For comparison, an acute dose of 5 to 10 Gy would kill a human **{** ADDIN EN.CITE <EndNote><Cite><Author>Hall</Author><Year>2011</Year><RecNum>8098</RecNum><record><rec-number>8098</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8098</key></foreign-keys><ref-type name="Book">6</ref-type><contributors><authors><author>Hall, E. J. </author><author>Giaccia, A. J. </author></authors></contributors><titles><title>Radiobiology for the Radiologist</title></titles><pages>576</pages><edition>7</edition><dates><year>2011</year></dates><publisher>Lippincott Williams & Wilkins</publisher><urls></urls></record></Cite></EndNote>**}** and 200 to 800 Gy would kill *E. coli* **{** ADDIN EN.CITE <EndNote><Cite><Author>Harris</Author><Year>2009</Year><RecNum>8099</RecNum><record><rec-number>8099</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8099</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Harris, Dennis R.</author><author>Pollock, Steve V.</author><author>Wood, Elizabeth A.</author><author>Goiffon, Reece J.</author><author>Klingele, Audrey J.</author><author>Cabot, Eric L.</author><author>Schackwitz, Wendy</author><author>Martin, Joel</author><author>Eggington, Julie</author><author>Durfee, Timothy J.</author><author>Middle, Christina M.</author><author>Norton, Jason E.</author><author>Popelars, Michael C.</author><author>Li, Hao</author><author>Klugman, Sarit A.</author><author>Hamilton, Lindsay L.</author><author>Bane, Lukas B.</author><author>Pennacchio, Len A.</author><author>Albert, Thomas J.</author><author>Perna, Nicole T.</author><author>Cox, Michael M.</author><author>Battista, John R.</author></authors></contributors><titles><title><style face="normal" font="default" size="100%">Directed evolution of ionizing radiation resistance in </style><style face="italic" font="default" size="100%">Escherichia coli</style></title><secondary-title>Journal of Bacteriology</secondary-title></titles><periodical><full-title>Journal of Bacteriology</full-title><abbr-1>J Bacteriol</abbr-1></periodical><pages>5240-5252</pages><volume>191</volume><number>16</number><dates><year>2009</year></dates><publisher>American Society for Microbiology (ASM)</publisher><isbn>0021-9193
1098-5530</isbn><accession-num>PMC2725583</accession-num><urls><related-urls><url>http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2725583/</url><url>http://jb.asm.org/content/191/16/5240.full.pdf</url></related-urls></urls><electronic-resource-num>10.1128/jb.00502-09</electronic-resource-num><remote-database-name>Pmc</remote-database-name></record></Cite></EndNote>**}**. When exposed to high doses of gamma radiation of up to 8,000 Gy, which are lethal for the majority of non-melanized fungi, melanized forms are able to survive, with melanin playing a role of a radioprotector **{** ADDIN EN.CITE

<EndNote><Cite><Author>Dadachova</Author><Year>2008</Year><RecNum>8012</RecNum><record><rec-number>8012</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8012</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Dadachova, E.</author><author>Bryan, R. A.</author><author>Howell, R. C.</author><author>Schweitzer, A. D.</author><author>Aisen, P.</author><author>Nosanchuk, J. D.</author><author>Casadevall, A.</author></authors></contributors><titles><title>The radioprotective properties of fungal melanin are a function of its chemical composition, stable radical presence and spatial arrangement</title><secondary-title>Pigment Cell & Melanoma Research</secondary-title></titles><periodical><full-title>Pigment Cell & Melanoma Research</full-title></periodical><pages>192-199</pages><volume>21</volume><number>2</number><dates><year>2008</year><pub-dates><date>Apr</date></pub-dates></dates><isbn>1755-1471</isbn><accession-num>WOS:000255061700013</accession-num><urls><related-urls><url><Go to ISI>://WOS:000255061700013</url></related-urls></urls><electronic-resource-num>10.1111/j.1755-148X.2007.00430.x</electronic-resource-num></record></Cite></EndNote>**}**. In addition, melanin protects the fungi *Cryptococcus neoformans* and *Cryomyces antarcticus* from highly energetic and damaging particulate radiation such as deuterons **{** ADDIN EN.CITE <EndNote><Cite><Author>Pacelli</Author><Year>2017</Year><RecNum>9000</RecNum><record><rec-number>9000</rec-number><foreign-keys><key app="EN" db-

id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">9000</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Pacelli, Claudia</author><author>Bryan, Ruth A.</author><author>Onofri, Silvano</author><author>Selbmann, Laura</author><author>Shuryak, Igor</author><author>Dadachova, Ekaterina</author></authors></contributors><titles><title>Melanin is effective in protecting fast and slow growing fungi from various types of ionizing radiation</title><secondary-title>Environmental Microbiology</secondary-title></titles><periodical><full-title>Environmental Microbiology</full-title><abbr-1>Environ Microbiol</abbr-1></periodical><pages>1612-1624</pages><volume>19</volume><number>4</number><dates><year>2017</year></dates><isbn>1462-2920</isbn><urls><related-urls><url>http://dx.doi.org/10.1111/1462-2920.13681</url></related-urls></urls><electronic-resource-num>10.1111/1462-2920.13681</electronic-resource-num></record></Cite></EndNote>**}**. Moreover, when exposed to non-lethal doses several times above the background radiation - melanized fungi grow better than their non-melanized counterparts **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}** implying that in such situations melanin plays a role as an energy transducer, allowing fungal cells to utilize the converted energy of ionizing radiation in their metabolic processes. The computer modeling of this dual relationship between melanized fungi and ionizing radiation revealed that these phenomena occur within a wide range of radiation doses, energies, and dose rates **{** ADDIN EN.CITE <EndNote><Cite><Author>Shuryak</Author><Year>2014</Year><RecNum>8011</R

ecNum><record><rec-number>8011</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8011</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Shuryak, I.</author><author>Bryan, R. A.</author><author>Nosanchuk, J. D.</author><author>Dadachova, E.</author></authors></contributors><titles><title>Mathematical modeling predicts enhanced growth of X-ray irradiated pigmented fungi</title><secondary-title>PLoS One</secondary-title></titles><periodical><full-title>PLoS One</full-title></periodical><volume>9</volume><number>1</number><dates><year>2014</year><pub-dates><date>Jan</date></pub-dates></dates><isbn>1932-6203</isbn><accession-num>WOS:000330235100098</accession-num><urls><related-urls><url><Go to ISI>://WOS:000330235100098</url></related-urls></urls><electronic-resource-num>10.1371/journal.pone.0085561</electronic-resource-num></record></Cite></EndNote>**}**. A possible mechanism of interaction between melanin in fungi and ionizing radiation involves Compton scattering of incident photons by the conjugated aromatic rings of the melanin structure with the simultaneous trapping of resulting Compton electrons by the melanin stable free radical **{** ADDIN EN.CITE
<EndNote><Cite><Author>Schweitzer</Author><Year>2009</Year><RecNum>8015</RecNum><record><rec-number>8015</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8015</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Schweitzer, A. D.</author><author>Howell, R.

C.</author><author>Jiang, Z. W.</author><author>Bryan, R. A.</author><author>Gerfen, G.</author><author>Chen, C. C.</author><author>Mah, D.</author><author>Cahill, S.</author><author>Casadevall, A.</author><author>Dadachova, E.</author></authors></contributors><titles><title>Physico-chemical evaluation of rationally designed melanins as novel nature-inspired radioprotectors</title><secondary-title>PLoS One</secondary-title></titles><periodical><full-title>PLoS One</full-title></periodical><volume>4</volume><number>9</number><dates><year>2009</year><pub-dates><date>Sep</date></pub-dates></dates><isbn>1932-6203</isbn><accession-num>WOS:000270354100003</accession-num><urls><related-urls><url><Go to ISI>://WOS:000270354100003</url></related-urls></urls><electronic-resource-num>10.1371/journal.pone.0007229</electronic-resource-num></record></Cite></EndNote>**}**. Electrochemical and electron spin resonance (ESR) investigations have demonstrated that melanin is oxidized during this process but is capable of self-repair by attracting electrons from the environment **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. Such unique properties of fungal melanin may have potential applications in radioprotection of patients undergoing radiation therapy **{** ADDIN EN.CITE

<EndNote><Cite><Author>Revskaya</Author><Year>2012</Year><RecNum>8018</RecNum><record><rec-number>8018</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8018</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Revskaya, E.</author><author>Chu, P.</author><author>Howell, R.

C.</author><author>Schweitzer, A. D.</author><author>Bryan, R. A.</author><author>Harris, M.</author><author>Gerfen, G.</author><author>Jiang, Z. W.</author><author>Jandl, T.</author><author>Kim, K.</author><author>Ting, L. M.</author><author>Sellers, R. S.</author><author>Dadachova, E.</author><author>Casadevall, A.</author></authors></contributors><titles><title>Compton scattering by internal shields based on melanin-containing mushrooms provides protection of gastrointestinal tract from ionizing radiation</title><secondary-title>Cancer Biotherapy and Radiopharmaceuticals</secondary-title></titles><periodical><full-title>Cancer Biotherapy and Radiopharmaceuticals</full-title></periodical><pages>570-576</pages><volume>27</volume><number>9</number><dates><year>2012</year><pub-dates><date>Nov</date></pub-dates></dates><isbn>1084-9785</isbn><accession-num>WOS:000310576000006</accession-num><urls><related-urls><url><Go to ISI>://WOS:000310576000006</url></related-urls></urls><electronic-resource-num>10.1089/cbr.2012.1318</electronic-resource-num></record></Cite></EndNote>**}**, in environmental remediation, and in creating genetically modified plants capable of using melanin and ionizing radiation in a process similar to photosynthesis **{** ADDIN EN.CITE <EndNote><Cite><Author>Dadachova</Author><Year>2008</Year><RecNum>7974</RecNum><record><rec-number>7974</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">7974</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Dadachova, E.</author><author>Casadevall, A.</author></authors></contributors><titles><title>Ionizing radiation: how fungi cope, adapt, and exploit with the help of melanin</title><secondary-title>Current Opinion in Microbiology</secondary-title></titles><periodical><full-title>Current Opinion in Microbiology</full-title></periodical><pages>525-531</pages><volume>11</volume><number>6</number><dates><year>2008</year><pub-dates><date>Dec</date></pub-dates></dates><isbn>1369-5274</isbn><accession-num>WOS:000261866200008</accession-num><urls><related-urls><url><Go to ISI>://WOS:000261866200008</url></related-urls></urls><electronic-resource-num>10.1016/j.mib.2008.09.013</electronic-resource-num></record></Cite></EndNote>**}**.

Solar ultraviolet radiation**:** Solar radiation is essential to life on Earth, but its UV component may also harm living organisms. Ultraviolet radiation was first separated into three wavelength categories at the Copenhagen Meeting of the Second International Congress on Light in 1932, dividing the UV spectrum into UV-C (shorter than 280 nm), UV-B (280 to 315 nm), and UV-A (315 to 400 nm) wavelengths **{** ADDIN EN.CITE <EndNote><Cite><Author>Coblentz</Author><Year>1932</Year><RecNum>8070</RecNum><record><rec-number>8070</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8070</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Coblentz, W. W.</author></authors></contributors><titles><title>The Copenhagen Meeting of the Second International Congress on Light</title><secondary-title>Science</secondary-title></titles><periodical><full-title>Science</full-title></periodical><pages>412-

5</pages><volume>76</volume><number>1975</number><edition>1932/11/04</edition><dates><year>1932</year><pub-dates><date>Nov 4</date></pub-dates></dates><isbn>0036-8075 (Print)
0036-8075 (Linking)</isbn><accession-num>17831918</accession-num><urls><related-urls><url>http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=17831918</url></related-urls></urls><electronic-resource-num>10.1126/science.76.1975.412</electronic-resource-num><language>eng</language></record></Cite></EndNote>**}**. Presently, however, many reports use 320 nm as the division between the UV-A and UV-B wavebands **{** ADDIN EN.CITE <EndNote><Cite><Author>Braga</Author><Year>2015</Year><RecNum>8262</RecNum><record><rec-number>8262</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8262</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Braga, G. U. L.</author><author>Rangel, D. E. N.</author><author>Fernandes, É. K. K.</author><author>Flint, S. D.</author><author>Roberts, D. W.</author></authors></contributors><titles><title>Molecular and physiological effects of environmental UV radiation on fungal conidia</title><secondary-title>Current Genetics</secondary-title><alt-title>Curr Genet</alt-title></titles><periodical><full-title>Current Genetics</full-title></periodical><alt-periodical><full-title>Curr Genet</full-title></alt-periodical><pages>405-425</pages><volume>61</volume><number>3</number><keywords><keyword>Fungal photobiology</keyword><keyword>UV tolerance</keyword><keyword>UV-induced damage</keyword><keyword>Microbial sunscreens</keyword><keyword>Conidia</keyword><keyword>Plant-pathogenic fungi</keyword><keyword>Insect-pathogenic fungi</keyword></keywords><dates><year>2015</year><pub-dates><date>2015/08/01</date></pub-dates></dates><publisher>Springer Berlin Heidelberg</publisher><isbn>0172-8083</isbn><urls><related-urls><url>http://dx.doi.org/10.1007/s00294-015-0483-0</url><url>http://download.springer.com/static/pdf/820/art%253A10.1007%252Fs00294-015-0483-0.pdf?originUrl=http%3A%2F%2Flink.springer.com%2Farticle%2F10.1007%2Fs00294-015-0483-0&token2=exp=1453231864~acl=%2Fstatic%2Fpdf%2F820%2Fart%25253A10.1007%25252Fs00294-015-0483-0.pdf%3ForiginUrl%3Dhttp%253A%252F%252Flink.springer.com%252Farticle%252F10.1007%252Fs00294-015-0483-0*~hmac=38fe081f6a73a32f61f507b87ad12823b273cc1a8bd36d08abc48d97b6102637</url></related-urls></urls><electronic-resource-num>10.1007/s00294-015-0483-0</electronic-resource-num><language>English</language></record></Cite></EndNote>**}**. UV-C radiation does not penetrate to the ground due to strong absorption by atmospheric gases including oxygen **{** ADDIN EN.CITE <EndNote><Cite><Author>Paul</Author><Year>2000</Year><RecNum>624</RecNum><record><rec-number>624</rec-number><foreign-keys><key app="EN" db-

id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">624</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Paul, N.D.</author></authors></contributors><titles><title>Stratospheric ozone depletion, UV-B radiation and crop disease</title><secondary-title>Environ. Pollut.</secondary-title></titles><pages>343-355</pages><volume>108</volume><dates><year>2000</year></dates><work-type>Paul, N.D. (2000). Stratospheric ozone depletion, UV-B radiation and crop disease. Environ. Pollut. 108, 343-355.</work-type><urls></urls></record></Cite></EndNote>**}**. The Earth’s surface is also largely protected from the most damaging short wavelength UV-B radiation due to absorption by stratospheric ozone. UV-A radiation passes through the atmosphere with little attenuation and is thus the largest component of ground-level solar UV radiation **{** ADDIN EN.CITE <EndNote><Cite><Author>Williamson</Author><Year>2014</Year><RecNum>8105</RecNum><record><rec-number>8105</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8105</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Williamson, Craig E.</author><author>Zepp, Richard G.</author><author>Lucas, Robyn M.</author><author>Madronich, Sasha</author><author>Austin, Amy T.</author><author>Ballare, Carlos L.</author><author>Norval, Mary</author><author>Sulzberger, Barbara</author><author>Bais, Alkiviadis F.</author><author>McKenzie, Richard L.</author><author>Robinson, Sharon A.</author><author>Hader, Donat-P.</author><author>Paul, Nigel D.</author><author>Bornman, Janet

F.</author></authors></contributors><titles><title>Solar ultraviolet radiation in a changing climate</title><secondary-title>Nature Clim. Change</secondary-title></titles><periodical><full-title>Nature Clim. Change</full-title></periodical><pages>434-441</pages><volume>4</volume><number>6</number><dates><year>2014</year></dates><publisher>Nature Publishing Group, a division of Macmillan Publishers Limited. All Rights Reserved.</publisher><isbn>1758-678X</isbn><work-type>Review</work-type><urls><related-urls><url>http://dx.doi.org/10.1038/nclimate2225</url></related-urls></urls><electronic-resource-num>10.1038/nclimate2225</electronic-resource-num></record></Cite></EndNote>**}**. The UV-B radiation from the sun may increase as a result of ozone depletion in the Earth's stratosphere, which is caused by man-made pollution **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. This increased solar UV-B radiation will have immense consequences for agriculture. Although plants are more tolerant to UV-B radiation than other organisms, it is known that UV-B radiation causes physiological changes (e.g. reduced net photosynthesis, changes in chemical composition, changes in pigment levels, premature ripening, and senescence) as well as morphological changes (e.g. increased branching, leaf thickness, and leaf size, as well as stunted growth) **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. In addition, increased solar UV-B radiation strongly affects microorganisms that are important for agriculture such as the plant pathogen antagonists *Trichoderma harzianum* and *Trichoderma viridae* **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**, fungi and bacteria used to control insect agricultural pests **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**, fungi to control insect vectors of disease **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**, and decomposer microorganisms { ADDIN EN.CITE { ADDIN EN.CITE.DATA }}. UV-B radiation can also change the species composition and biodiversity of bacterial and fungal communities growing on plants. For pathogens, elevated UV-B can either increase or decrease the severity of disease development in plants depending on the fungal-plant-pathogenic species { ADDIN EN.CITE { ADDIN EN.CITE.DATA }}.

High temperatures**:** Another source of stress is the heat produced by solar irradiation or convection. Depending on the soil type, solar heat may cause the temperature of the bare-soil within 5 cm of the surface to reach temperatures of up to 65 °C - this phenomenon has been reported during the rainy season in the Niger Republic, West Africa { ADDIN EN.CITE
<EndNote><Cite><Author>Arthurs</Author><Year>2001</Year><RecNum>8140</RecNum><record><rec-number>8140</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8140</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Arthurs, S. P.</author><author>Thomas, M. B.</author><author>Lawton, J. L.</author></authors></contributors><titles><title><style face="normal" font="default" size="100%">Seasonal patterns of persistence and infectivity of </style><style face="italic" font="default" size="100%">Metarhizium anisopliae</style><style face="normal" font="default" size="100%"> var. </style><style face="italic" font="default" size="100%">acridum</style><style face="normal" font="default" size="100%"> in grasshopper cadavers in the Sahel</style></title><secondary-title>Entomologia Experimentalis et Applicata</secondary-

title></titles><periodical><full-title>Entomologia Experimentalis et Applicata</full-title></periodical><pages>69-76</pages><volume>100</volume><number>1</number><keywords><keyword>Metarhizium anisopliae var. acridum</keyword><keyword>entomopathogenic fungi</keyword><keyword>microbial control</keyword><keyword>locusts and grasshoppers</keyword><keyword>horizontal transmission</keyword></keywords><dates><year>2001</year></dates><publisher>Blackwell Science Ltd</publisher><isbn>1570-7458</isbn><urls><related-urls><url>http://dx.doi.org/10.1046/j.1570-7458.2001.00849.x</url></related-urls></urls><electronic-resource-num>10.1046/j.1570-7458.2001.00849.x</electronic-resource-num></record></Cite></EndNote>**}**. Bare soil surfaces subjected to full sunlight reached 60 °C in irrigated corn fields in Logan, Utah, USA in mid-July at 5:00 pm **{** ADDIN EN.CITE <EndNote><Cite><Author>Rangel</Author><Year>2005</Year><RecNum>628</RecNum><record><rec-number>628</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">628</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Rangel, D.E.N.</author><author>Braga, G.U.L.</author><author>Anderson, A.J.</author><author>Roberts, D.W.</author></authors></contributors><titles><title><style face="normal" font="default" size="100%">Variability in conidial thermotolerance of </style><style face="italic" font="default" size="100%">Metarhizium anisopliae</style><style face="normal" font="default" size="100%"> isolates from different geographic origins</style></title><secondary-title>Journal of Invertebrate Pathology</secondary-title></titles><periodical><full-title>Journal of Invertebrate Pathology</full-title></periodical><pages>116-125</pages><volume>88</volume><dates><year>2005</year></dates><work-type>J. Invertebr. Pathol.</work-type><urls></urls></record></Cite></EndNote>**}**. Thus, resistance to heat represents an important adaptive trait for many microbial communities. Usually germlings and mycelia are much more susceptible to heat **{** ADDIN EN.CITE <EndNote><Cite><Author>Rangel</Author><Year>2010</Year><RecNum>4450</RecNum><record><rec-number>4450</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">4450</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Rangel, D. E. N.</author><author>Fernandes, E.K.K.</author><author>Dettenmaier, S.J. </author><author>Roberts, D.W.</author></authors></contributors><titles><title><style face="normal" font="default" size="100%">Thermotolerance of germlings and mycelium of the insect-pathogenic fungus </style><style face="italic" font="default" size="100%">Metarhizium</style><style face="normal" font="default" size="100%"> spp. and mycelial recovery after heat stress</style></title><secondary-title>Journal of Basic Microbiology</secondary-title><short-title>J. Basic. Microbiol</short-title></titles><periodical><full-title>Journal of Basic Microbiology</full-title><abbr-1>J Basic Microb</abbr-1></periodical><pages>344–350</pages><volume>50</volume><dates><year>2010</year></dates><urls></urls></record></Cite></EndNote>**}** than their counterpart conidia **{** ADDIN EN.CITE **{** ADDIN

EN.CITE.DATA **}}**. Heat stress has great influence on soil microbes; for example, isolates of insect-pathogenic fungi *Metarhizium* spp. collected from above latitude 40° North or South are less heat tolerant than isolates collected from close to the equator **{** ADDIN EN.CITE <EndNote><Cite><Author>Rangel</Author><Year>2005</Year><RecNum>628</RecNum><record><rec-number>628</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">628</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Rangel, D.E.N.</author><author>Braga, G.U.L.</author><author>Anderson, A.J.</author><author>Roberts, D.W.</author></authors></contributors><titles><title><style face="normal" font="default" size="100%">Variability in conidial thermotolerance of </style><style face="italic" font="default" size="100%">Metarhizium anisopliae</style><style face="normal" font="default" size="100%"> isolates from different geographic origins</style></title><secondary-title>Journal of Invertebrate Pathology</secondary-title></titles><periodical><full-title>Journal of Invertebrate Pathology</full-title></periodical><pages>116-125</pages><volume>88</volume><dates><year>2005</year></dates><work-type>J. Invertebr. Pathol.</work-type><urls></urls></record></Cite></EndNote>**}**. In addition, a population genetics analysis of the insect-pathogenic fungus *Metarhizium anisopliae* from forested and agricultural habitats in Ontario, Canada found that the group from forested areas has an ability for cold-active growth at 8 °C and is less tolerant to heat, while the group from the agricultural area showed an ability for growth at high temperatures at 37 °C and they are less cold-active **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. Man-made global warming is predicted to increase the annual mean surface temperature of earth even more; this will, no doubt, bring extreme changes in the Earth's surface microbial populations. Allison et al. **{** ADDIN EN.CITE <EndNote><Cite ExcludeAuth="1"><Author>Allison</Author><Year>2010</Year><RecNum>8117</RecNum><record><rec-number>8117</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8117</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Allison, SD</author><author>McGire, KL</author><author>Treseder, KK</author></authors></contributors><titles><title>Resistance of microbial and soil properties to warming treatment seven years after boreal fire</title><secondary-title>Soil Biology and Biochemistry</secondary-title></titles><periodical><full-title>Soil Biology and Biochemistry</full-title></periodical><pages>1872**–**1878</pages><volume>42</volume><number>10</number><dates><year>2010</year></dates><urls></urls></record></Cite></EndNote>**}** pointed out a different effect of heat: burning of a boreal fire can deplete carbon from soil. This, in turn, increased the resistance of a fungal community to soil warming. Similarly, fungal communities from sand mining degraded soil, which is carbon depleted and intensely heated, are more heat and UV-B tolerant than the fungal communities after the ecological restoration of this same area with native trees **{** ADDIN EN.CITE <EndNote><Cite><Author>Ferreira</Author><Year>2017</Year><RecNum>8847</RecNum><record><rec-number>8847</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8847</key></foreign-keys><ref-type

name="Journal Article">17</ref-type><contributors><authors><author>Ferreira, Paulo C.</author><author>Pupin, Breno</author><author>Rangel, Drauzio E. N.</author></authors></contributors><titles><title>Stress tolerance of soil fungal communities from native Atlantic forests, reforestations, and a sand mining degraded area</title><secondary-title>Fungal Biology</secondary-title></titles><periodical><full-title>Fungal Biology</full-title><abbr-1>Fungal Biol-Uk</abbr-1></periodical><keywords><keyword>soil fungal community</keyword><keyword>ecosystem services</keyword><keyword>UV-B tolerance</keyword><keyword>heat tolerance</keyword><keyword>cold activity</keyword><keyword>ecological restoration</keyword><keyword>reforestation</keyword><keyword>Atlantic forest</keyword><keyword>sand mining degraded soil</keyword></keywords><dates><year>2017</year></dates><isbn>1878-6146</isbn><urls><related-urls><url>http://www.sciencedirect.com/science/article/pii/S1878614617300880</url></related-urls></urls><electronic-resource-num>10.1016/j.funbio.2017.07.002</electronic-resource-num></record></Cite></EndNote>**}**.

Cold temperatures**:** Fungi can be isolated from extremely cold environments, including permafrost, deep seas, snow and polar environments (Gunde-Cimerman *et al*. 2003). Physiological mechanisms conferring cold tolerance in fungi are complex and include increases in intracellular trehalose and polyols, and unsaturated membrane lipids as well as secretion of antifreeze proteins and possession of enzymes active at low temperatures

(Robinson 2001). Furthermore, fungi with dark septate hyphae may dominate the microbial community in Antarctic, Arctic and alpine soils. Melanins may protect these organisms from extreme temperatures and drought, and play a significant role for persistence of hyphae from year to year in such environments (Robinson 2001). Cold-adapted fungi are a potential source for novel bioactive secondary metabolites and enzymes (Rateb & Ebel 2011; Wang *et al*. 2015).

Acidity and alkalinity**:** One of the most influential factors that can affect microbial communities in soil is pH since it strongly influences nutrient availability and metal mobility, and community composition of fungi and bacteria. In general, acidic pH values favour fungal growth which results in an increase in the dominance and relative importance of fungi compared to bacteria under acidic soil conditions such as in coniferous soil. Apart from this, many fungi can grow over a wide pH range from extreme acidity to alkaline conditions (Magan 2007). Many alkalitolerant and alkaliphilic species are known (pH 8-11), isolated from alkaline environments such as soda soils, calcareous deposits, and ammonia and urea-enriched soils (Grum-Grzhimaylo *et al*. 2016; Li *et al*. 2015). Alkaliphily may be associated with morphological responses such as darkly pigmented mycelium, formation of microsclerotia or other enclosed fruit bodies, extensive production of extracellular polymeric materials (EPS), and hyphal aggregation in chords (Grum-Grzhimaylo *et al*. 2016). Furthermore, fungi, including lichens, are important biodeteriogens in the built environment and are well known to have significant effects even on alkaline substrates such as concrete, cement, mortars and plaster (Fomina *et al*. 2007; Gadd 2017b). It is now known that many fungi inhabit extremely acidic environments, including yeasts and filamentous forms (Gross & Robbins 2000; Baker *et al*. 2004; Aguilera *et al*. 2006). Some filamentous species isolated from acidic environments are some of the most acidophilic microorganisms that have been documented, e.g. *Acontium cylatium, Trichosporon cerebriae* and a *Cephalosporium* sp. have all been reported to grow at around pH 0 (Schleper *et al.* 1995; Aguilera *et al*. 2006; Magan 2007). The physiological basis for alkaliphily or acidophily in fungi has received scant attention, although there is evidence for vacuolar involvement in H^+ homeostasis under extreme acidity (Magan 2007). A *Penicillium ochro-chloron* strain capable of growth in high concentrations of copper sulfate at very low pH synthesised high amounts of glycerol allowing growth in such conditions, with copper uptake being greatly repressed under such low acidity (Gadd *et al*. 1984; Gadd & White 1985).

Osmotic stress: In several environments fungi will encounter hyperosmolarity and low water potentials caused by the presence of high concentrations of salts and sugars. Fungi are found in several natural locations such as alkaline soda Wadi El-Natrun Lakes in Egypt **{** ADDIN EN.CITE

<EndNote><Cite><Author>Moubasher</Author><Year>2013</Year><RecNum>8570</RecNum><record><rec-number>8570</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8570</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Moubasher, A. H.</author><author>Ismail, M. A.</author><author>Hussein, N. A.</author><author>Gouda, H. A.

A.</author></authors></contributors><titles><title>Terrestrial fungi tolerating the
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>**}**, or in the alkaline and hypersaline Mono Lake in California, USA **{** ADDIN EN.CITE
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L.</author><author>Guiraud, P.</author></authors></contributors><auth-
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0003-6072 (Linking)</isbn><accession-num>15028878</accession-num><urls><related-urls><url>http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=15028878</url></related-urls></urls><electronic-resource-num>10.1023/B:ANTO.0000020150.91058.4d</electronic-resource-num><language>Eng</language></record></Cite></EndNote>**}** and on the Dead Sea shore located in the Syrian-African rift valley, on the border between Israel and Jordan **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. The ability to survive osmotic stress requires several adaptations in fungi involving osmoregulation **{** ADDIN EN.CITE <EndNote><Cite><Author>Hohmann</Author><Year>2002</Year><RecNum>8573</RecNum><record><rec-number>8573</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8573</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Hohmann, S.</author></authors></contributors><auth-address>Department of Cell and Molecular Biology/Microbiology, Goteborg University, S-405 30 Goteborg, Sweden. hohmann@gmm.gu.se</auth-address><titles><title>Osmotic stress signaling and osmoadaptation in yeasts</title><secondary-title>Microbiol Mol Biol Rev</secondary-title></titles><periodical><full-title>Microbiol Mol Biol Rev</full-title></periodical><pages>300-

72</pages><volume>66</volume><number>2</number><edition>2002/06/01</edition><keywords><keyword>Adaptation, Physiological</keyword><keyword>Amino Acid Sequence</keyword><keyword>Cyclic AMP-Dependent Protein Kinases/metabolism</keyword><keyword>Feedback</keyword><keyword>Fungal Proteins/genetics/metabolism</keyword><keyword>Genes, Fungal</keyword><keyword>Glycerol/metabolism</keyword><keyword>Intracellular Signaling Peptides and Proteins</keyword><keyword>Mitogen-Activated Protein Kinases/metabolism</keyword><keyword>Models, Biological</keyword><keyword>Molecular Sequence Data</keyword><keyword>Osmotic Pressure</keyword><keyword>*Protein Kinases</keyword><keyword>Saccharomyces cerevisiae Proteins/metabolism</keyword><keyword>Signal Transduction</keyword><keyword>Transcription Factors/genetics/metabolism</keyword><keyword>Yeasts/genetics/*metabolism</keyword></keywords><dates><year>2002</year><pub-dates><date>Jun</date></pub-dates></dates><isbn>1092-2172 (Print)
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Dias, M. C.</author><author>Ramos, J.</author></authors></contributors><auth-address>Departamento de Microbiologia, Escuela Tecnica Superior de Ingenieros Agronomos, E-14071 Cordoba, Spain.</auth-address><titles><title><style face="normal" font="default" size="100%">Cloning and expression of two genes coding for sodium pumps in the salt-tolerant yeast </style><style face="italic" font="default" size="100%">Debaryomyces hansenii</style></title><secondary-title>J Bacteriol</secondary-title></titles><periodical><full-title>J Bacteriol</full-title></periodical><pages>3251-5</pages><volume>183</volume><number>10</number><edition>2001/04/28</edition><keywords><keyword>Adenosine Triphosphatases/genetics/*metabolism</keyword><keyword>*Cation Transport Proteins</keyword><keyword>*Cloning, Molecular</keyword><keyword>Hydrogen-Ion Concentration</keyword><keyword>Molecular Sequence Data</keyword><keyword>*Saccharomyces cerevisiae Proteins</keyword><keyword>Saccharomycetales/*genetics/growth & development/metabolism</keyword><keyword>Sodium Chloride/*metabolism</keyword><keyword>Sodium-Potassium-Exchanging ATPase/genetics/*metabolism</keyword></keywords><dates><year>2001</year><pub-dates><date>May</date></pub-dates></dates><isbn>0021-9193 (Print)
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num>10.1128/JB.183.10.3251-3255.2001</electronic-resource-num><language>Eng</language></record></Cite></EndNote>}, and melanin synthesis { ADDIN EN.CITE { ADDIN EN.CITE.DATA }}. Under these conditions, fungi adjust their internal solute potentials by accumulation of solutes such as glycerol, erythritol, mannitol, and trehalose, which reduces internal water potential and limits osmotic losses { ADDIN EN.CITE { ADDIN EN.CITE.DATA }}. In addition, they modify the plasma membrane { ADDIN EN.CITE

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rane Fluidity/drug effects</keyword><keyword>Membrane Lipids/*metabolism</keyword><keyword>Phospholipids/metabolism</keyword><keyword>Sodium Chloride/*pharmacology</keyword><keyword>Species Specificity</keyword><keyword>Sterols/metabolism</keyword></keywords><dates><year>2004</year><pub-dates><date>Feb</date></pub-dates></dates><isbn>1431-0651 (Print)
1431-0651 (Linking)</isbn><accession-num>15064990</accession-num><urls><related-urls><url>http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=15064990</url><url>http://link.springer.com/article/10.1007%2Fs00792-003-0360-5</url></related-urls></urls><electronic-resource-num>10.1007/s00792-003-0360-5</electronic-resource-num><language>Eng</language></record></Cite></EndNote>**}**, increase cell wall thickness **{** ADDIN EN.CITE <EndNote><Cite><Author>Kralj Kuncic</Author><Year>2010</Year><RecNum>8586</RecNum><record><rec-number>8586</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8586</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Kralj Kuncic, M.</author><author>Kogej, T.</author><author>Drobne, D.</author><author>Gunde-Cimerman, N.</author></authors></contributors><auth-address>Department of Biology, Biotechnical Faculty, University of Ljubljana, Vecna Pot 111, SI-1000 Ljubljana, Slovenia.</auth-address><titles><title>Morphological response of the halophilic fungal genus Wallemia to high salinity</title><secondary-title>Appl Environ Microbiol</secondary-title></titles><periodical><full-title>Appl Environ

Microbiol</full-title></periodical><pages>329-37</pages><volume>76</volume><number>1</number><edition>2009/11/10</edition><keywords><keyword>Antifungal Agents/*pharmacology</keyword><keyword>Basidiomycota/*cytology/drug effects/*physiology</keyword><keyword>Cell Wall/drug effects</keyword><keyword>Culture Media/chemistry</keyword><keyword>Microscopy</keyword><keyword>Microscopy, Electron, Scanning</keyword><keyword>Microscopy, Electron, Transmission</keyword><keyword>*Osmotic Pressure</keyword><keyword>*Salinity</keyword><keyword>Salts/*pharmacology</keyword><keyword>*Stress, Physiological</keyword></keywords><dates><year>2010</year><pub-dates><date>Jan</date></pub-dates></dates><isbn>1098-5336 (Electronic)
0099-2240 (Linking)</isbn><accession-num>19897760</accession-num><urls><related-urls><url>http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=19897760</url><url>http://aem.asm.org/content/76/1/329.full.pdf</url></related-urls></urls><custom2>2798636</custom2><electronic-resource-num>10.1128/AEM.02318-09</electronic-resource-num><language>Eng</language></record></Cite></EndNote>**}** and in some cases, as observed in halotolerant fungi such as *Cladosporium cladosporioides,* they accumulate mycosporines **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. Osmotic stress also causes an increase in fatty acid unsaturation in the membranes **{** ADDIN EN.CITE <EndNote><Cite><Author>Turk</Author><Year>2004</Year><RecNum>8588</RecN

um><record><rec-number>8588</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8588</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Turk, M.</author><author>Mejanelle, L.</author><author>Sentjurc, M.</author><author>Grimalt, J. O.</author><author>Gunde-Cimerman, N.</author><author>Plemenitas, A.</author></authors></contributors><auth-address>Institute of Biochemistry, Medical Faculty, University of Ljubljana, Vrazov trg 2, 1000, Ljubljana, Slovenia.</auth-address><titles><title>Salt-induced changes in lipid composition and membrane fluidity of halophilic yeast-like melanized fungi</title><secondary-title>Extremophiles</secondary-title></titles><periodical><full-title>Extremophiles</full-title></periodical><pages>53-61</pages><volume>8</volume><number>1</number><edition>2004/04/06</edition><keywords><keyword>Ascomycota/*drug effects/isolation & purification/*metabolism</keyword><keyword>Electron Spin Resonance Spectroscopy</keyword><keyword>Melanins/metabolism</keyword><keyword>Membrane Fluidity/drug effects</keyword><keyword>Membrane Lipids/*metabolism</keyword><keyword>Phospholipids/metabolism</keyword><keyword>Sodium Chloride/*pharmacology</keyword><keyword>Species Specificity</keyword><keyword>Sterols/metabolism</keyword></keywords><dates><year>2004</year><pub-dates><date>Feb</date></pub-dates></dates><isbn>1431-0651 (Print)
1431-0651 (Linking)</isbn><accession-num>15064990</accession-num><urls><related-urls><url>http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubM

ed&dopt=Citation&list_uids=15064990</url><url>http://link.springer.com/article/10.1007%2Fs00792-003-0360-5</url></related-urls></urls><electronic-resource-num>10.1007/s00792-003-0360-5</electronic-resource-num><language>Eng</language></record></Cite></EndNote>**}**, as well as modifications in the morphology of fungal cells **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}** and colonies **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**.

Some fungal species are known to be halotolerant, osmotolerant, or xerotolerant. Such fungi includes the melanized *Cladosporium* species, that are found in hypersaline waters around the world **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. *Cladosporium* has also been found in other extreme habitats, such as stratosphere **{** ADDIN EN.CITE <EndNote><Cite><Author>Della Corte</Author><Year>2014</Year><RecNum>8392</RecNum><record><rec-number>8392</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8392</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Della Corte, V.</author><author>Rietmeijer, F. J.</author><author>Rotundi, A.</author><author>Ferrari, M.</author></authors></contributors><auth-address>1 Istituto di Astrofisica e Planetologia Spaziali-INAF , Roma, Italy .</auth-address><titles><title>Introducing a new stratospheric dust-collecting system with potential use for upper atmospheric microbiology investigations</title><secondary-title>Astrobiology</secondary-title></titles><periodical><full-title>Astrobiology</full-title></periodical><pages>694-705</pages><volume>14</volume><number>8</number><edition>2014/07/22</edition

><keywords><keyword>*Air Microbiology</keyword><keyword>*Atmosphere</keyword><keyword>Dust/*analysis</keyword><keyword>Microbiology/instrumentation</keyword></keywords><dates><year>2014</year><pub-dates><date>Aug</date></pub-dates></dates><isbn>1557-8070 (Electronic)
1557-8070 (Linking)</isbn><accession-num>25046407</accession-num><urls><related-urls><url>http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=25046407</url></related-urls></urls><custom2>4126274</custom2><electronic-resource-num>10.1089/ast.2014.1167</electronic-resource-num><language>eng</language></record></Cite></EndNote>**}**, or rocks of the Atacama Desert **{** ADDIN EN.CITE <EndNote><Cite><Author>Gonçalves</Author><Year>2016</Year><RecNum>8437</RecNum><record><rec-number>8437</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8437</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Gonçalves, Vívian N.</author><author>Cantrell, Charles L.</author><author>Wedge, David E.</author><author>Ferreira, Mariana C.</author><author>Soares, Marco Aurélio</author><author>Jacob, Melissa R.</author><author>Oliveira, Fabio S.</author><author>Galante, Douglas</author><author>Rodrigues, Fabio</author><author>Alves, Tânia M. A.</author><author>Zani, Carlos L.</author><author>Junior, Policarpo A. S.</author><author>Murta, Silvane</author><author>Romanha, Alvaro J.</author><author>Barbosa, Emerson

C.</author><author>Kroon, Erna G.</author><author>Oliveira, Jaquelline G.</author><author>Gomez-Silva, Benito</author><author>Galetovic, Alexandra</author><author>Rosa, Carlos A.</author><author>Rosa, Luiz H.</author></authors></contributors><titles><title>Fungi associated with rocks of the Atacama Desert: taxonomy, distribution, diversity, ecology and bioprospection for bioactive compounds</title><secondary-title>Environmental Microbiology</secondary-title></titles><periodical><full-title>Environmental Microbiology</full-title><abbr-1>Environ Microbiol</abbr-1></periodical><pages>232-245</pages><volume>18</volume><number>1</number><dates><year>2016</year></dates><isbn>1462-2920</isbn><urls><related-urls><url>http://dx.doi.org/10.1111/1462-2920.13005</url><url>http://onlinelibrary.wiley.com/doi/10.1111/1462-2920.13005/abstract</url></related-urls></urls><electronic-resource-num>10.1111/1462-2920.13005</electronic-resource-num></record></Cite></EndNote>**}**, which are known to have a very low water activity. Another member of indigenous fungal communities in hypersaline waters of salterns, includes the genus *Eurotium*, **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}** that can grow at 0.70 water activity (a_w) **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}** and even lower **{** ADDIN EN.CITE <EndNote><Cite><Author>Stevenson</Author><Year>2015</Year><RecNum>8069</RecNum><record><rec-number>8069</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8069</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Stevenson, Andrew</author><author>Cray, Jonathan A.</author><author>Williams, Jim P.</author><author>Santos, Ricardo</author><author>Sahay, Richa</author><author>Neuenkirchen, Nils</author><author>McClure, Colin D.</author><author>Grant, Irene R.</author><author>Houghton, Jonathan D. R.</author><author>Quinn, John P.</author><author>Timson, David J.</author><author>Patil, Satish V.</author><author>Singhal, Rekha S.</author><author>Anton, Josefa</author><author>Dijksterhuis, Jan</author><author>Hocking, Ailsa D.</author><author>Lievens, Bart</author><author>Rangel, Drauzio E. N.</author><author>Voytek, Mary A.</author><author>Gunde-Cimerman, Nina</author><author>Oren, Aharon</author><author>Timmis, Kenneth N.</author><author>McGenity, Terry J.</author><author>Hallsworth, John E.</author></authors></contributors><titles><title>Is there a common water-activity limit for the three domains of life?</title><secondary-title>ISME J</secondary-title></titles><periodical><full-title>ISME J</full-title></periodical><pages>1333–1351</pages><volume>9</volume><dates><year>2015</year></dates><publisher>International Society for Microbial Ecology</publisher><isbn>1751-7370</isbn><work-type>Original Article</work-type><urls><related-urls><url>http://dx.doi.org/10.1038/ismej.2014.219</url></related-urls></urls><electronic-resource-num>10.1038/ismej.2014.219</electronic-resource-num></record></Cite></EndNote>**}**. Another extreme halophile is the fungus *Aspergillus penicilliodes*, which is able to germinate at 0.585 a_w (approximately 58.5% relative humidity), which is now considered the limit for life **{** ADDIN EN.CITE

<EndNote><Cite><Author>Stevenson</Author><Year>2017</Year><RecNum>9098</RecNum><record><rec-number>9098</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">9098</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Stevenson, Andrew</author><author>Hamill, Philip G.</author><author>O'Kane, Callum J.</author><author>Kminek, Gerhard</author><author>Rummel, John D.</author><author>Voytek, Mary A.</author><author>Dijksterhuis, Jan</author><author>Hallsworth, John E.</author></authors></contributors><titles><title><style face="italic" font="default" size="100%">Aspergillus penicillioides</style><style face="normal" font="default" size="100%"> differentiation and cell division at 0.585 water activity</style></title><secondary-title>Environmental Microbiology</secondary-title></titles><periodical><full-title>Environmental Microbiology</full-title><abbr-1>Environ Microbiol</abbr-1></periodical><pages>687-697</pages><volume>19</volume><number>2</number><dates><year>2017</year></dates><isbn>1462-2920</isbn><urls><related-urls><url>http://dx.doi.org/10.1111/1462-2920.13597</url></related-urls></urls><electronic-resource-num>10.1111/1462-2920.13597</electronic-resource-num></record></Cite></EndNote>**}**.

Toxic metals**:** Anthropogenic activities, including fossil fuel combustion, mineral mining and processing, release of industrial effluents and sludges, biocides and preservatives, redistribute a variety of toxic metal species into aquatic and terrestrial ecosystems which can have significant effects on the biota (Gadd 2016). In addition, metals are involved in almost all geomicrobial processes, and their transformations and alterations in mobility are important in bioweathering, mineral formation and dissolution, and soil formation (Gadd 2010). Metals, metalloids, metal radionuclides, organometals and organometalloids, and their compounds, interact with fungi in various ways depending on chemical speciation, organism and environment, with the fungi also able to influence metal speciation and mobility (Gadd *et al*. 2012; Gadd 2017a, 2018). Many metals are essential for life, e.g. Na, K, Cu, Zn, Co, Ca, Mg, Mn, and Fe, but all can be potentially toxic when present above certain threshold concentrations. Other metals, e.g. Cs, Al, Cd, Hg and Pb, have no known metabolic function in fungi but can still be accumulated. Metal toxicity is affected by physico-chemical conditions and the chemical behaviour of the particular metal species (Gadd 1993; Howlett & Avery 1997; Fomina *et al.* 2005). However, fungi are ubiquitous in metal-polluted locations and a variety of direct and indirect mechanisms contribute to their survival. Such mechanisms include reduction of metal uptake and/or increased efflux, metal immobilization by, e.g. biosorption to cell walls and exoploymers, mineral bioprecipitation, intracellular sequestration, and localization in vacuoles (Gadd 1993, 2007, 2010). Such mechanisms by which fungi (and other microorganisms) change metal speciation and mobility not only influences survival but are also important components of biogeochemical cycles for metals, and other elements that may be associated with organic and inorganic substrates including carbon, nitrogen, sulfur and phosphorus (Gadd 2004, 2006, 2007, 2008). In some cases, wall structure and composition is affected by the presence of toxic metals and this may in turn influence colony development and morphology (Ramsay *et al*. 1999). A variety of toxic metals can induce or accelerate melanin production in fungi, leading to blackening of colonies and chlamydospore development (Gadd & Griffiths 1980). Melanized forms have high capacities for metal biosorption, with the majority of metal remaining within the wall structure (Gadd 1984; Gadd & Mowll 1985; Gadd *et al*. 1987). Synnema are defined as aerial, multihyphal structures where the apices of the component hyphae advance together and ultimately form spores (Watkinson 1979). They are therefore concerned with the spread and survival of a given species and their formation can be triggered by a variety of external factors and stresses, e.g. light-dark transitions, low temperature, alcohols, detergents, carbon dioxide, amino acids and certain metal compounds (Watkinson 1979; Newby & Gadd 1987).

Xenobiotics: Fungi, as well as other microorganisms, encounter a broad spectrum of antimicrobial compounds in their environments and often possess metabolic strategies to detoxify such xenobiotics. These can include anthropogenic pollutants such as pesticides, polycyclic aromatic hydrocarbons (PAH), and other persistent organic pollutants (POP), as well as many antifungal substances produced by a broad spectrum of organisms (Tincu & Taylor 2004; Jenssen *et al*. 2006). The latter compounds include peptides, fatty acids, proteins, alkaloids, quinones, and statins. Survival necessitates expression of effective antitoxin mechanisms and the most common processes used by fungi in resistance to antifungal agents are destruction of the agent, changes in the target enzyme or pathway by mutation, and active efflux to maintain low intracellular concentrations (Ghannoum & Rice 1999; Cowen & Steinbach 2008; Barabote *et al*. 2011). Some fungi have remarkable degradative properties and lignin-degrading white rot fungi, such as

Phanerochaete chrysosporium, can degrade several xenobiotics including aromatic hydrocarbons, chlorinated organics, polychlorinated biphenyls, nitrogen-containing aromatics and many other pesticides, dyes and other xenobiotic (Gadd 2004; Magan *et al*. 2010). Such behaviour is of relevance to bioremediation of such substances although co-metabolism of a more easily utilisable carbon source may be additionally required, as well as beneficial interactions with bacterial communities (Gadd 2004).

***Rock and mineral-based substrates*:** Due to their filamentous growth habit and ability to produce and exude organic acids, protons and other metabolites, fungi are ideal biological weathering agents of rocks, minerals and building materials. Fungi are ubiquitous components of the microbiota of all rocks and building stone and they have been reported from a wide range of rock types including limestone, marble, granite, sandstone, basalt, gneiss, dolerite and quartz, even from the most harsh environments, e.g. hot and cold deserts (Staley *et al*. 1982; Gorbushina 2007; Sterflinger 2000; Verrecchia 2000). Furthermore, fungi are considered to be the most important colonizers of stone, mortar and plaster (Sterflinger 2000, 2009; Scheerer et al. 2009). Sub-aerial rock surfaces may be thought an inhospitable habitat for fungal growth due to moisture deficit and nutrient limitation although many species are able to deal with varying extremes in such factors as light, nutrient availability, salinity, pH, and water potential, over considerable periods of time. The presence of organic and inorganic residues on mineral surfaces or within cracks and fissures within the mineral substrate can encourage proliferation of fungi and other microbes as well as the waste products of algae and bacteria, dead cells, decaying plant material, dust particles, aerosols and animal faeces (Sterflinger 2000). The ability of many fungi to grow oligotrophically by scavenging nutrients from the air and rainwater also helps them survive on stone and rock surfaces (Wainwright *et al*. 1993; Gorbushina 2007). Stone-inhabiting microorganisms may grow on the surface (epilithic), in crevices and fissures (chasmolithic), or may penetrate some millimetres or even centimetres into the rock pore system (endolithic), thereby gaining protection from environmental extremes and fluctuations (Hoppert *et al*. 2004; Gorbushina 2007; Gadd 2017c). Some fungal groups exhibit microcolonial or yeast-like growth forms that are effective in providing protection from heat and desiccation (Gorbushina 2007). These may prevail under harsh conditions, and appear as black spots due to possession of UV-protective melanins (Gorbushina 2007; Gorbushina & Broughton 2009). This growth habit confers a high degree of resistance to environmental stresses and these organisms are considered the most persistent inhabitants of exposed rock surfaces. One of the most successful means for fungi to survive in the extreme sub-aerial environment is underpinned by their symbiotic associations with algae and cyanobacteria as lichens where the phototrophs provide a source of carbon and protection from light and irradiation (Sterflinger 2000). Lichens enable colonization of a wide range of environments including those at climatic extremes such as the Arctic and Antarctic, exposed rock surfaces and dry deserts (Gadd 2017c).

Deep subsurface**:** In the deep subsurface, the research emphasis is mostly on prokaryotes, but the presence of fungi is now well known (Ivarsson 2012; Nagano & Nagahama 2012; Orsi et al. 2013; Ivarsson *et al*. 2016). Fungi occur in abundance and high diversity in such varied environments as deep-sea sediments (Nagano *et al*. 2010), hydrothermal vents (Connell *et al*. 2009; Le Calvez *et al*. 2009), and methane cold-seeps (Nagano *et al*. 2010; Nagahama *et al*. 2011). They are now also known as abundant inhabitants of the igneous oceanic crust which has consequently been described as the largest fungal habitat on Earth (Ivarsson *et al*. 2016). Fungi seem to play an important ecological role in the igneous oceanic crust as they exist in symbiosis with chemolithotrophic prokaryotes, decompose organic matter, dissolve and form minerals, and therefore are involved in the cycling of elements (Bengtson *et al*. 2014; Ivarsson *et al*. 2015, 2016). Fossilized microorganisms have been observed in drilled cores and dredged samples from the ocean floor with a majority of these findings representing fungi (Schumann *et al*. 2004; Bengtson *et al*. 2014). These fungi existed in a close symbiotic-like relationship with two types of prokaryotes, which appeared to use the structural framework of the mycelium for their growth (Bengtson *et al*. 2014). It therefore seems clear that geomycological processes are significant in a wide range of biosphere habitats, including those traditionally thought to be inimical to fungal growth and development (Gadd 2006).

Fungal Stress in Agriculture and Forestry: Many important pathogens of crop plants in forestry and agriculture are fungi but fungi are also increasingly used as commercial biological control agents to control plant diseases { ADDIN EN.CITE <EndNote><Cite><Author>Butt</Author><Year>2001</Year><RecNum>8102</RecNum><record><rec-number>8102</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8102</key></foreign-keys><ref-type name="Book">6</ref-type><contributors><authors><author>Butt,

T.M.</author><author>Jackson, C.</author><author>Magan, N. </author></authors></contributors><titles><title> Fungi as biocontrol agents: progress, problems and potential</title></titles><dates><year>2001</year></dates><pub-location>Wallingford, UK.</pub-location><publisher>CABI Publishing</publisher><urls></urls></record></Cite></EndNote> } . In coniferous forests *Heterobasidion* fungi cause economically devastating root rot diseases causing financial losses of 790 M € each year in Europe alone. However, application of the fungus *Phlebiopsis gigantea* to root stumps during tree felling can result in 95-100% reduction of the disease with little apparent impact on other soil fungi { ADDIN EN.CITE

<EndNote><Cite><Author>Menkis</Author><Year>2012</Year><RecNum>8103</RecNum><record><rec-number>8103</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8103</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Menkis, Audrius</author><author>Burokienė, Daiva</author><author>Gaitnieks, Talis</author><author>Uotila, Antti</author><author>Johannesson, Hanna</author><author>Rosling, Anna</author><author>Finlay, Roger D.</author><author>Stenlid, Jan</author><author>Vasaitis, Rimvydas</author></authors></contributors><titles><title><style face="normal" font="default" size="100%">Occurrence and impact of the root-rot biocontrol agent </style><style face="italic" font="default" size="100%">Phlebiopsis gigantea</style><style face="normal" font="default" size="100%"> on soil fungal communities in </style><style face="italic" font="default" size="100%">Picea

abies</style><style face="normal" font="default" size="100%"> forests of northern Europe</style></title><secondary-title>FEMS Microbiology Ecology</secondary-title></titles><periodical><full-title>FEMS Microbiology Ecology</full-title></periodical><pages>438-445</pages><volume>81</volume><number>2</number><keywords><keyword>Phlebiopsis gigantea</keyword><keyword>biocontrol</keyword><keyword>environmental impact</keyword><keyword>fungal ecology</keyword><keyword>soil fungi</keyword></keywords><dates><year>2012</year></dates><isbn>1574-6941</isbn><urls><related-urls><url>http://dx.doi.org/10.1111/j.1574-6941.2012.01366.x</url></related-urls></urls><electronic-resource-num>10.1111/j.1574-6941.2012.01366.x</electronic-resource-num></record></Cite></EndNote>**}**. Biocontrol has typically been approached from the point of view of how antagonists attack pathogens and there are far fewer studies of how fungal pathogens respond to the biological stress induced by antagonists **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. These self-defense responses are diverse, including detoxification, repression of synthetic biocontrol genes, active efflux of antibiotics, and antibiotic resistance. A better understanding of the mechanisms involved will aid the development of more efficient antagonists. Many fungi have been developed into commercial biological control agents and are being mass produced to be used in agriculture to promote plant growth **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**, promote plant defense responses **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**, and to control plant diseases **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**, plant parasitic nematodes **{** ADDIN EN.CITE

<EndNote><Cite><Author>Siddiqui</Author><Year>1996</Year><RecNum>7995</RecNum><record><rec-number>7995</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">7995</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Siddiqui, Z. A.</author><author>Mahmood, I.</author></authors></contributors><auth-address>Siddiqui, ZA (reprint author), ALIGARH MUSLIM UNIV, DEPT BOT, ALIGARH 202002, UTTAR PRADESH, INDIA.</auth-address><titles><title>Biological control of plant parasitic nematodes by fungi: A review</title><secondary-title>Bioresource Technology</secondary-title><alt-title>Bioresour. Technol.</alt-title></titles><periodical><full-title>Bioresource Technology</full-title><abbr-1>Bioresource Technol</abbr-1></periodical><pages>229-239</pages><volume>58</volume><number>3</number><keywords><keyword>biological control</keyword><keyword>fungi</keyword><keyword>plant parasitic nematodes</keyword><keyword>production and</keyword><keyword>formulation of fungi</keyword><keyword>cereal cyst-nematode</keyword><keyword>meloidogyne-arenaria eggs</keyword><keyword>verticillium-chlamydosporium</keyword><keyword>paecilomyces-lilacinus</keyword><keyword>hirsutella-rhossiliensis</keyword><keyword>heterodera-avenae</keyword><keyword>control agent</keyword><keyword>phytonematode pathology</keyword><keyword>pratylenchus-penetrans</keyword><keyword>nematophagous

fungi</keyword></keywords><dates><year>1996</year><pub-dates><date>Dec</date></pub-dates></dates><isbn>0960-8524</isbn><accession-num>WOS:A1996WK59100002</accession-num><work-type>Review</work-type><urls><related-urls><url><Go to ISI>://WOS:A1996WK59100002</url></related-urls></urls><electronic-resource-num>10.1016/s0960-8524(96)00122-8</electronic-resource-num><language>English</language></record></Cite></EndNote>**}**, terrestrial weeds **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**, aquatic weeds **{** ADDIN EN.CITE <EndNote><Cite><Author>Cother</Author><Year>1994</Year><RecNum>8010</RecNum><record><rec-number>8010</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8010</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Cother, E. J.</author><author>Gilbert, R. L.</author></authors></contributors><titles><title><style face="normal" font="default" size="100%">Pathogenicity of </style><style face="italic" font="default" size="100%">Rhynchosporium alismatis</style><style face="normal" font="default" size="100%"> and its potential as a mycoherbicide on several weed species in the Alismataceae</style></title><secondary-title>Australian Journal of Experimental Agriculture</secondary-title></titles><periodical><full-title>Australian Journal of Experimental Agriculture</full-title></periodical><pages>1039-1042</pages><volume>34</volume><number>7</number><dates><year>1994</year></dates><isbn>0816-1089</isbn><accession-num>WOS:A1994QH43900024</accession-num><urls><related-urls><url><Go to

ISI>://WOS:A1994QH43900024</url></related-urls></urls><electronic-resource-num>10.1071/ea9941039</electronic-resource-num></record></Cite></EndNote>**}**, and insects **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}** **}** . Different abiotic environmental factors cause stress and consequently harm these important fungi in agricultural systems, and fungi that are applied to the aerial parts of plants, such as insect pathogens, are especially susceptible to solar UV radiation **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}** and heat **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}** that cause reductions in their activity. Fungi that control weeds (mycoherbistats) are also affected by UV-B radiation **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**.

Symbiotic mycorrhizal fungi play important roles in stress tolerance in both agricultural and forest ecosystems, improving nutrient uptake and drought tolerance, restricting base cation leaching and mitigating the toxic effects of elevated heavy metals and aluminum **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. Different types of mycorrhizal symbiosis have very different effects in different systems and carbon allocated by the plants to their fungal symbionts may be used for fungal production of siderophores or enzymes used to mobilize organic polymers of nitrogen or phosphorus, glycoproteins that stabilize soil aggregates, or priming of bacteria involved in solubilizing phosphorus or other types of plant growth promotion **{** ADDIN EN.CITE <EndNote><Cite><Author>Finlay</Author><Year>2008</Year><RecNum>8120</RecNum><record><rec-number>8120</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8120</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Finlay, R. D.</author></authors></contributors><auth-address>Department of Forest Mycology and Pathology, Uppsala BioCenter, SLU, Box 7026, Uppsala SE-750 07, Sweden. Roger.Finlay@mykopat.slu.se</auth-address><titles><title>Ecological aspects of mycorrhizal symbiosis: with special emphasis on the functional diversity of interactions involving the extraradical mycelium</title><secondary-title>J Exp Bot</secondary-title><alt-title>Journal of experimental botany</alt-title></titles><periodical><full-title>J Exp Bot</full-title></periodical><alt-periodical><full-title>Journal of Experimental Botany</full-title></alt-periodical><pages>1115-26</pages><volume>59</volume><number>5</number><keywords><keyword>Bacterial Physiological Phenomena</keyword><keyword>Biodegradation, Environmental</keyword><keyword>Carbon</keyword><keyword>*Ecosystem</keyword><keyword>Minerals/metabolism</keyword><keyword>Mycelium/*physiology</keyword><keyword>Mycorrhizae/*physiology</keyword><keyword>Organic Chemicals/metabolism</keyword><keyword>Plant Physiological Phenomena</keyword><keyword>Plant Roots/microbiology</keyword><keyword>*Symbiosis</keyword></keywords><dates><year>2008</year></dates><isbn>1460-2431 (Electronic)
0022-0957 (Linking)</isbn><accession-num>18349054</accession-num><urls><related-urls><url>http://www.ncbi.nlm.nih.gov/pubmed/18349054</url><url>http://jxb.oxfordjournals.org/content/59/5/1115.full.pdf</url></related-urls></urls><electronic-resource-num>10.1093/jxb/ern059</electronic-resource-num></record></Cite></EndNote> } . Carbon flow in the rhizosphere or “mycorrhizosphere” may have important consequences for mitigation of effects of plant diseases or interactions with decomposers and thus be of significance in the sustainability of low-input cropping systems { ADDIN EN.CITE {

ADDIN EN.CITE.DATA }}. Fungi may also influence global patterns of carbon sequestration. Clemmensen et al. { ADDIN EN.CITE <EndNote><Cite ExcludeAuth="1"><Author>Clemmensen</Author><Year>2013</Year><RecNum>8122</RecNum><record><rec-number>8122</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8122</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Clemmensen, K. E.</author><author>Bahr, A.</author><author>Ovaskainen, O.</author><author>Dahlberg, A.</author><author>Ekblad, A.</author><author>Wallander, H.</author><author>Stenlid, J.</author><author>Finlay, R. D.</author><author>Wardle, D. A.</author><author>Lindahl, B. D.</author></authors></contributors><auth-address>Department of Forest Mycology and Plant Pathology, Uppsala BioCenter, Swedish University of Agricultural Sciences, Uppsala, Sweden. karina.clemmensen@slu.se</auth-address><titles><title>Roots and associated fungi drive long-term carbon sequestration in boreal forest</title><secondary-title>Science</secondary-title><alt-title>Science</alt-title></titles><periodical><full-title>Science</full-title></periodical><alt-periodical><full-title>Science</full-title></alt-periodical><pages>1615-8</pages><volume>339</volume><number>6127</number><keywords><keyword>Biological Markers/metabolism</keyword><keyword>*Carbon Cycle</keyword><keyword>Carbon Radioisotopes/metabolism</keyword><keyword>Ergosterol/metabolism</keyword><keyword>Fungi/*metabolism</keyword><keyword>Glucosamine/metabolism</keyword>

<keyword>Plant Roots/*metabolism/*microbiology</keyword><keyword>Soil</keyword><keyword>Trees/*metabolism/*microbiology</keyword></keywords><dates><year>2013</year><pub-dates><date>Mar 29</date></pub-dates></dates><isbn>1095-9203 (Electronic)
0036-8075 (Linking)</isbn><accession-num>23539604</accession-num><urls><related-urls><url>http://www.ncbi.nlm.nih.gov/pubmed/23539604</url></related-urls></urls><electronic-resource-num>10.1126/science.1231923</electronic-resource-num></record></Cite></EndNote>} demonstrated that at least half of the accumulated carbon in humus layers of boreal forested islands originated from root-derived inputs rather than from above-ground plant litter inputs. More recent results of Clemmensen et al. { ADDIN EN.CITE <EndNote><Cite ExcludeAuth="1"><Author>Clemmensen</Author><Year>2015</Year><RecNum>8123</RecNum><record><rec-number>8123</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8123</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Clemmensen, K. E.</author><author>Finlay, R. D.</author><author>Dahlberg, A.</author><author>Stenlid, J.</author><author>Wardle, D. A.</author><author>Lindahl, B. D.</author></authors></contributors><auth-address>Department of Forest Mycology and Plant Pathology, Uppsala BioCenter, Swedish University of Agricultural Sciences, Box 7026, SE-75007, Uppsala, Sweden.</auth-address><titles><title>Carbon sequestration is related to mycorrhizal fungal community shifts during long-term

succession in boreal forests</title><secondary-title>New Phytol</secondary-title><alt-title>The New phytologist</alt-title></titles><periodical><full-title>New Phytologist</full-title><abbr-1>New Phytol</abbr-1></periodical><pages>1525-36</pages><volume>205</volume><number>4</number><dates><year>2015</year><pub-dates><date>Mar</date></pub-dates></dates><isbn>1469-8137 (Electronic)
0028-646X (Linking)</isbn><accession-num>25494880</accession-num><urls><related-urls><url>http://www.ncbi.nlm.nih.gov/pubmed/25494880</url></related-urls></urls><electronic-resource-num>10.1111/nph.13208</electronic-resource-num></record></Cite></EndNote>**}** suggest that at earlier successional stages, the high abundance of cord-forming ectomycorrhizal fungi implies efficient recycling of carbon and nitrogen, whereas in older ecosystems, stress-adapted, root-associated ascomycetes generally seem to promote biochemical stabilization of these compounds in organic matter derived from mycelium. Recent studies of arbuscular mycorrhiza in agricultural systems suggest that AM fungi improve drought tolerance and tolerance of salinity of their plant hosts through improved nutrient uptake, accumulation of organic solutes and reduced oxidative stress due to enhanced activity of calmodulin, superoxide dismutase, catalase, peroxidase, and ascorbate peroxidase **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**.

Assigning trophic strategies to filamentous fungi is complicated by the fact that their mycelia may simultaneously interact with different substrates in different ways. An example of this is the entomopathogenic fungus *Metarhizium robertsii* that can transfer insect-derived N to plants, promoting their growth **{** ADDIN EN.CITE

<EndNote><Cite><Author>Behie</Author><Year>2012</Year><RecNum>7986</RecNum><record><rec-number>7986</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">7986</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Behie, S. W.</author><author>Zelisko, P. M.</author><author>Bidochka, M. J.</author></authors></contributors><titles><title>Endophytic insect-parasitic fungi translocate nitrogen directly from insects to plants</title><secondary-title>Science</secondary-title></titles><periodical><full-title>Science</full-title></periodical><pages>1576-1577</pages><volume>336</volume><number>6088</number><dates><year>2012</year><pub-dates><date>Jun</date></pub-dates></dates><isbn>0036-8075</isbn><accession-num>WOS:000305507500056</accession-num><urls><related-urls><url><Go to ISI>://WOS:000305507500056</url></related-urls></urls><electronic-resource-num>10.1126/science.1222289</electronic-resource-num></record></Cite></EndNote>**}** while this process is driven by reciprocal allocation of C from the plant roots to the fungal mycelium **{** ADDIN EN.CITE

<EndNote><Cite><Author>Behie</Author><Year>2017</Year><RecNum>9173</RecNum><record><rec-number>9173</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">9173</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Behie, Scott W.</author><author>Moreira, Camila C.</author><author>Sementchoukova, Irina</author><author>Barelli, Larissa</author><author>Zelisko, Paul M.</author><author>Bidochka, Michael

J.</author></authors></contributors><titles><title>Carbon translocation from a plant to an insect-pathogenic endophytic fungus</title><secondary-title>Nature Communications</secondary-title></titles><periodical><full-title>Nature Communications</full-title></periodical><pages>14245</pages><volume>8</volume><dates><year>2017</year></dates><publisher>The Author(s)</publisher><work-type>Article</work-type><urls><related-urls><url>http://dx.doi.org/10.1038/ncomms14245</url></related-urls></urls><electronic-resource-num>10.1038/ncomms14245</electronic-resource-num></record></Cite></EndNote>**}**.

A recent study by Liao et al. **{** ADDIN EN.CITE <EndNote><Cite ExcludeAuth="1"><Author>Liao</Author><Year>2014</Year><RecNum>8135</RecNum><record><rec-number>8135</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8135</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Liao, Xinggang</author><author>O'Brien, TammathaR</author><author>Fang, Weiguo</author><author>St. Leger, RaymondJ</author></authors></contributors><titles><title><style face="normal" font="default" size="100%">The plant beneficial effects of </style><style face="italic" font="default" size="100%">Metarhizium</style><style face="normal" font="default" size="100%"> species correlate with their association with roots</style></title><secondary-title>Applied Microbiology and Biotechnology</secondary-title><alt-title>Appl Microbiol Biotechnol</alt-title></titles><periodical><full-title>Applied Microbiology and Biotechnology</full-

title></periodical><alt-periodical><full-title>Appl Microbiol Biotechnol</full-title></alt-periodical><pages>7089-7096</pages><volume>98</volume><number>16</number><keywords><keyword>Plant-microbe interaction</keyword><keyword>Corn yield</keyword><keyword>Plant biofertilizer</keyword><keyword>Rhizospheric insect pathogen</keyword><keyword>Metarhizium species</keyword></keywords><dates><year>2014</year><pub-dates><date>2014/08/01</date></pub-dates></dates><publisher>Springer Berlin Heidelberg</publisher><isbn>0175-7598</isbn><urls><related-urls><url>http://dx.doi.org/10.1007/s00253-014-5788-2</url></related-urls></urls><electronic-resource-num>10.1007/s00253-014-5788-2</electronic-resource-num><language>English</language></record></Cite></EndNote>**}** using *Zea mays* colonization of plant roots by different wild type and mutant *Metarhizium* strains suggested that the fungi were plant growth promoters irrespective of their role as insect pathogens and that colonization of roots was a pre-requisite for most if not all of their beneficial effects. Other groups of (non-mycorrhizal) fungi that are well-known for mediating stress reactions in plants include species of the genus *Trichoderma*, which show a wide range of lifestyles but are able to antagonize or parasitize plant-pathogenic fungi and to stimulate plant growth and defense responses **{** ADDIN EN.CITE <EndNote><Cite><Author>Druzhinina</Author><Year>2011</Year><RecNum>8232</RecNum><record><rec-number>8232</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8232</key></foreign-keys><ref-type name="Journal Article">17</ref-

type><contributors><authors><author>Druzhinina, Irina S.</author><author>Seidl-Seiboth, Verena</author><author>Herrera-Estrella, Alfredo</author><author>Horwitz, Benjamin A.</author><author>Kenerley, Charles M.</author><author>Monte, Enrique</author><author>Mukherjee, Prasun K.</author><author>Zeilinger, Susanne</author><author>Grigoriev, Igor V.</author><author>Kubicek, Christian P.</author></authors></contributors><titles><title><style face="italic" font="default" size="100%">Trichoderma</style><style face="normal" font="default" size="100%">: the genomics of opportunistic success</style></title><secondary-title>Nat Rev Micro</secondary-title></titles><periodical><full-title>Nat Rev Micro</full-title></periodical><pages>749-759</pages><volume>9</volume><number>10</number><dates><year>2011</year></dates><publisher>Nature Publishing Group, a division of Macmillan Publishers Limited. All Rights Reserved.</publisher><isbn>1740-1526</isbn><work-type>10.1038/nrmicro2637</work-type><urls><related-urls><url>http://dx.doi.org/10.1038/nrmicro2637</url></related-urls></urls></record></Cite></EndNote>**}**, and species such as *Piriformospora indica,* which can promote the growth of a spectrum of plants by inducing disease resistance and tolerance of salt stress through a systemic elevation of the antioxidative capacity mediated by the glutathione-ascorbate cycle **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. There is growing interest in plant biostimulants to enhance plant growth **{** ADDIN EN.CITE

<EndNote><Cite><Author>Calvo</Author><Year>2014</Year><RecNum>8136</RecNum><record><rec-number>8136</rec-number><foreign-keys><key app="EN" db-

id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8136</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Calvo, Pamela</author><author>Nelson, Louise</author><author>Kloepper, JosephW</author></authors></contributors><titles><title>Agricultural uses of plant biostimulants</title><secondary-title>Plant and Soil</secondary-title><alt-title>Plant Soil</alt-title></titles><periodical><full-title>Plant and Soil</full-title><abbr-1>Plant Soil</abbr-1></periodical><alt-periodical><full-title>Plant and Soil</full-title><abbr-1>Plant Soil</abbr-1></alt-periodical><pages>3-41</pages><volume>383</volume><number>1-2</number><keywords><keyword>Microbial inoculants</keyword><keyword>Humic acid</keyword><keyword>Fulvic acid</keyword><keyword>Protein hydrolysates</keyword><keyword>Amino acids</keyword><keyword>Seaweed extracts</keyword><keyword>Biostimulants</keyword></keywords><dates><year>2014</year><pub-dates><date>2014/10/01</date></pub-dates></dates><publisher>Springer International Publishing</publisher><isbn>0032-079X</isbn><urls><related-urls><url>http://dx.doi.org/10.1007/s11104-014-2131-8</url></related-urls></urls><electronic-resource-num>10.1007/s11104-014-2131-8</electronic-resource-num><language>English</language></record></Cite></EndNote>} and clear potential for exploiting fungal stress responses to access novel molecules that can be used in agriculture. Fungal endophytes have also been discussed as an important reservoir of novel antibacterial substances with therapeutic potential { ADDIN EN.CITE <EndNote><Cite><Author>Deshmukh</Author><Year>2014</Year><RecNum>8126</

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1664-302X (Linking)</isbn><accession-num>25620957</accession-num><urls><related-urls><url>http://www.ncbi.nlm.nih.gov/pubmed/25620957</url></related-urls></urls><custom2>4288058</custom2><electronic-resource-num>10.3389/fmicb.2014.00715</electronic-resource-num></record></Cite></EndNote>**}**. Induction of tolerance to heat stress in naturally growing plants colonized by fungal endophytes **{** ADDIN EN.CITE <EndNote><Cite><Author>Redman</Author><Year>2002</Year><RecNum>8127</RecNum><record><rec-number>8127</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8127</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Redman, R.

S.</author><author>Sheehan, K. B.</author><author>Stout, R. G.</author><author>Rodriguez, R. J.</author><author>Henson, J. M.</author></authors></contributors><auth-address>U.S. Geological Survey, WFRC, 6505 NE 65th Street, Seattle, WA 98115, USA.</auth-address><titles><title>Thermotolerance generated by plant/fungal symbiosis</title><secondary-title>Science</secondary-title><alt-title>Science</alt-title></titles><periodical><full-title>Science</full-title></periodical><alt-periodical><full-title>Science</full-title></alt-periodical><pages>1581</pages><volume>298</volume><number>5598</number><keywords><keyword>Ascomycota/growth & development/isolation & purification/*physiology</keyword><keyword>*Hot Temperature</keyword><keyword>Plant Leaves/microbiology</keyword><keyword>Plant Roots/microbiology/physiology</keyword><keyword>Poaceae/growth & development/*microbiology/*physiology</keyword><keyword>Seeds/microbiology</keyword><keyword>Soil</keyword><keyword>Soil Microbiology</keyword><keyword>Spores, Fungal/physiology</keyword><keyword>*Symbiosis</keyword></keywords><dates><year>2002</year><pub-dates><date>Nov 22</date></pub-dates></dates><isbn>1095-9203 (Electronic)
0036-8075 (Linking)</isbn><accession-num>12446900</accession-num><urls><related-urls><url>http://www.ncbi.nlm.nih.gov/pubmed/12446900</url></related-urls></urls><electronic-resource-num>10.1126/science.1072191</electronic-resource-

num></record></Cite></EndNote>**}** has also been shown to occur in wheat, increasing grain yield, seed germination, and drought tolerance **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**. Other more recent studies of symbiotically conferred stress tolerance **{** ADDIN EN.CITE

<EndNote><Cite><Author>Rodriguez</Author><Year>2008</Year><RecNum>8129</RecNum><record><rec-number>8129</rec-number><foreign-keys><key app="EN" db-id="0w99vfvvswpf2bewxab50vpvr9f0xsar9avw">8129</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Rodriguez, R. J.</author><author>Henson, J.</author><author>Van Volkenburgh, E.</author><author>Hoy, M.</author><author>Wright, L.</author><author>Beckwith, F.</author><author>Kim, Y. O.</author><author>Redman, R. S.</author></authors></contributors><auth-address>US Geological Survey, WFRC, Seattle, WA, USA.</auth-address><titles><title>Stress tolerance in plants via habitat-adapted symbiosis</title><secondary-title>ISME J</secondary-title><alt-title>The ISME journal</alt-title></titles><periodical><full-title>ISME J</full-title></periodical><pages>404-16</pages><volume>2</volume><number>4</number><keywords><keyword>*Adaptation, Physiological</keyword><keyword>*Ecosystem</keyword><keyword>Fusarium/classification/genetics/*growth & development/isolation & purification</keyword><keyword>*Heat-Shock Response</keyword><keyword>Hot Temperature</keyword><keyword>Lycopersicon esculentum/growth & development/microbiology/physiology</keyword><keyword>Oryza sativa/growth

& development/microbiology/physiology</keyword><keyword>Poaceae/growth & development/*microbiology/physiology</keyword><keyword>Sodium Chloride/pharmacology</keyword><keyword>*Symbiosis</keyword><keyword>Washington</keyword></keywords><dates><year>2008</year><pub-dates><date>Apr</date></pub-dates></dates><isbn>1751-7362 (Print)
1751-7362 (Linking)</isbn><accession-num>18256707</accession-num><urls><related-urls><url>http://www.ncbi.nlm.nih.gov/pubmed/18256707</url></related-urls></urls><electronic-resource-num>10.1038/ismej.2007.106</electronic-resource-num></record></Cite></EndNote>**}** suggest that it arises as a result of habitat-adapted symbiosis and that it may have considerable potential in mitigating impacts of climate change in different cropping systems, as well as expanding agricultural production onto marginal lands **{** ADDIN EN.CITE **{** ADDIN EN.CITE.DATA **}}**.

In conclusion, fungi perform important functions in a variety of natural processes, including effects on soil fertility and plant productivity, decomposition of organic matter, cycling of minerals, plant health, and food production and consumption. Successful exploitation of fungi requires better understanding of the mechanisms that fungi use to cope with stress, as well as of the ways in which they mediate stress tolerance in other organisms.

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